Feeding biology and diversity of oribatid mites (Oribatida, Acari)

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Katja Schneider

aus Darmstadt

Referent: Prof. Dr. Stefan Scheu

Koreferent: Dr. habil. Michael Bonkowski

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‘The truth is in here somewhere’
Robbie Williams

Carabodes femoralis

Mites are most easily recognised by what they are not – other arachnids.

Walter and Proctor (1999)

PUBLICATIONS RESULTING FROM THIS DISSERTATION

CHAPTER 2.1.

Schneider K, Migge S, Norton RA, Scheu S, Langel R, Reineking A, Maraun M (2004) Trophic niche differentiation in oribatid mites (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/^{14}N$). Soil Biology and Biochemistry 36, 1769-1774

CHAPTER 2.2.

Schneider K and Maraun M (2005) Feeding preferences among dark pigmented fungi ("Dematiacea") indicate trophic niche differentiation of oribatid mites. Pedobiologia 49, 61-67

CHAPTER 2.3.

Schneider K and Maraun M (2005) Oribatid mite (Oribatida, Acari) feeding on ectomycorrhizal fungi. Mycorrhiza (submitted)

CHAPTER 2.4.

Maraun M, Salamon J-A, Schneider K, Schaefer M, Scheu S (2003) Oribatid mite and collembolan diversity, density and community structure in a moder beech forest (*Fagus sylvatica*): effects of mechanical perturbations. Soil Biology and Biochemistry 35, 1387-1394

CHAPTER 2.5.

Salamon J-A, Alphei J, Ruf A, Schaefer M, Scheu S, Schneider K, Sührig A, Maraun M (2005) Transitory dynamic effects in the soil invertebrate community in a temperate deciduous forest: effects of resource quality. Soil Biology and Biochemistry (in press)

FURTHER PUBLICATIONS

Schneider K, Renker C, Scheu S, Maraun M (2004) Feeding biology of oribatid mites: a minireview. Phytophaga (in press)

Schneider K, Scheu S, Maraun M (2005) Animal density and diversity in soil responds little to spatial isolation. Basic and Applied Ecology (submitted)

Maraun M, Heethoff M, Schneider K, Scheu S, Weigmann G, Cianciolo J, Thomas RH, Norton RA (2004) Molecular phylogeny of oribatid mites (Oribatida, Acari): evidence for multiple radiations of parthenogenetic lineages. Experimental and Applied Acarology 33, 183-201

Renker C, Otto P, Zimdars B, Schneider K, Maraun M, Buscot F (2005) Oribatid mites as potential vectors for soil microfungi. Microbial Ecology (in press)

Schäfer I, Domes K, Heethoff M, Schneider K, Norton RA, Scheu S, Maraun M (2004) No evidence for the 'Meselson effect' in parthenogenetic oribatid mites (Oribatida, Acari). Journal of Evolutionary Biology (in press)

ZUSAMMENFASSUNG

Ziel der vorliegenden Arbeit war es, die Mechanismen zu verstehen, die die Koexistenz einer Vielzahl an Hornmilbenarten (Oribatida, Acari) ermöglichen, die ohne deutliche Nischendifferenzierung im Boden leben. Im Rahmen dieser Arbeit habe ich in zwei Nahrungswahlexperimenten, einer stabilen Isotopenanalyse (^{15}N) und zwei Freilandexperimenten drei Mechanismen untersucht, die die hohe Diversität von Hornmilben erklären könnten: trophische Einnischung, Störung und Nahrungsmenge bzw. -qualität.

Bodenmikroarthropoden, wie zum Beispiel Springschwänze und Hornmilben, fressen bevorzugt an dunkel pigmentierten Pilzen (‚Dematiacea'). In einem Nahrungswahlversuch habe ich die Nahrungspräferenzen von zehn Hornmilben für acht ‚Dematiacea' untersucht. Die untersuchten Hornmilbenarten fraßen zwar signifikant unterschiedlich an den jeweiligen Pilzarten, generell bevorzugten sie jedoch alle die gleichen Pilze (*Alternaria alternata* und *Ulocladium* sp.). Hornmilben sind also hinsichtlich der Nahrungsresource ‚Dematiacea' nur schwach eingenischt. Diese geringe Einnischung kann jedoch zumindest einen Teil der hohen Diversität der Hornmilben erklären.

Mykorrhizapilze erreichen im Waldboden hohe Dichten und stellen eine potenzielle Nahrungsresource für Hornmilben dar. Daher habe ich in einem Nahrungswahlexperiment drei Hornmilbenarten sechs Ektomykorrhizapilze und einen ericoiden Mykorrhizapilz als Nahrung angeboten. Die untersuchten Hornmilbenarten unterschieden sich signifikant in ihren Nahrungspräferenzen, allgemein bevorzugten sie jedoch zwei Mykorrhizapilze, *Hymenoscyphus ericae* und *Boletus badius*. Diese Ergebnisse weisen darauf hin, dass es trophische Einnischung innerhalb der Hornmilben gibt. Diese ist jedoch hinsichtlich der Mykorrhizapilze nicht deutlich genug, um die hohe Anzahl koexistierender Hornmilbenarten zu erklären.

Die trophische Nischendifferenzierung von 36 Hornmilbenarten/-taxa aus vier Wäldern wurde mit Hilfe der Analyse der natürlichen Variation des stabilen Stickstoffisotops (^{15}N) untersucht. Die untersuchten Hornmilbenarten ließen sich in vier trophische Gruppen einteilen. Dabei bildeten sie einen Gradienten von Pflanzenfressern über Primär- und Sekundärzersetzer bis hin zu Räubern und Aasfressern. Diese überraschend großen Unterschiede in den ^{15}N-Werten unterstützen die Befunde der trophischen Einnischung von Hornmilben der Laborversuche. Die Ergebnisse dieser Analyse deuten stark darauf hin, dass Nischendifferenzierung hinsichtlich der Nahrung eine wichtige Rolle für die Koexistenz von Hornmilben und damit für die Diversität dieser Tiergruppe spielt.

Die ‚intermediate disturbance hypothesis' besagt, dass die Diversität von Pflanzen und Tieren bei mittlerer Störungsintensität am höchsten ist. Daher habe ich die Auswirkung von drei Störungsintensitäten (einmalige Störung, Störung alle zwei Monate und Störung alle zwei Wochen) auf die Diversität und Dichte von Hornmilben untersucht. Dabei nahm ich an, dass die Artenzahl in den Behandlungen mit mittlerer Störungsintensität (Störung alle zwei Monate) am höchsten ist. Im Gegensatz zu dieser Annahme nahm die Diversität der Hornmilben in allen drei Störungsbehandlungen ab. Diese Ergebnisse deuten darauf hin, dass nahezu alle Hornmilbenarten empfindlich gegenüber Störungen sind, und dass die ‚intermediate disturbance hypothesis' nicht auf Hornmilben anwendbar ist. Allgemein kann man sagen, dass die Diversität von Hornmilben nicht von Störungen profitiert.

Der Einfluss der temporären Erhöhung der Verfügbarkeit von Nahrung unterschiedlicher Qualität (Holz, Glukose & Stickstoff & Phosphor (CNP), Tierfutter, Weizenkleie) auf Hornmilben wurde in einem Freilandexperiment im Solling (Deutschland) untersucht. Ich nahm an, dass die Diversität der Hornmilben mit der Nahrungsquantität und –qualität ansteigt. Die Ergebnisse dieses Experimentes konnten diese Hypothese jedoch nicht bestätigen, da die Artenzahl der Hornmilben sich nicht zwischen den Behandlungen mit erhöhter Ressourcenqualität bzw. -quantität und der

Kontrolle unterschied. Die Dichte der Hornmilben war jedoch in der CNP-Behandlung im Vergleich zur Tierfutter-Behandlung leicht erhöht. Dies ist jedoch eher ein indirekter Effekt, der aus der Abnahme der Regenwurmdichte in der CNP-Behandlung resultiert. Die Ergebnisse deuten darauf hin, dass Hornmilbengemeinschaften nicht durch die Nahrungsmenge oder –qualität limitiert sind, sondern eher durch die Grab-Aktivitäten von Regenwürmern. Die Menge und Qualität von Ressourcen trägt daher nicht zur hohen Diversität von Hornmilben bei.

Zusammenfassend deuten die Ergebnisse der vorliegenden Arbeit darauf hin, dass die Koexistenz der Vielzahl an Hornmilbenarten im Boden nicht von dem Auftreten von Störungen mittlerer Intensität oder von der Nahrungsmenge abhängt, sondern sich durch die trophische Einnischung der verschiedenen Hornmilbenarten erklären lässt. Ein Vergleich der Ergebnisse der Nahrungswahlexperimente und der stabilen Isotopenanalyse zeigt, dass Hornmilben im Labor an einer Vielzahl von verschiedenen Ressourcen fressen, im Freiland jedoch unterschiedliche Nahrungsnischen besetzen. Um diese Nahrungsnischen besser zu verstehen, sind weitere Untersuchungen der Nahrungsbiologie von Hornmilben nötig. Moderne Techniken, wie z.B. die Analyse von Phospholipidfettsäuren oder die Darmanalyse mit Hilfe molekularer Methoden, können in Zukunft wesentlich zum Verständnis der trophischen Nischendifferenzierung von Hornmilben beitragen.

SUMMARY

The aim of this study was to understand the regulatory mechanism of the high diversity of soil living oribatid mites (Acari, Oribatida) which appear to coexist without extensive niche differentiation. I focussed on trophic niche differentiation, perturbation and resource quantity and quality as three putative mechanisms. Two food choice experiments, one stable isotope analysis and two field experiments were conducted.

Dark pigmented fungi ('Dematiacea') are generally preferred as diet by soil microarthropods, such as collembolans and oribatid mites. I investigated the feeding preferences of ten oribatid mite species among eight 'Dematiacea' in a food choice experiment. The investigated oribatid mite species differentially fed on dark pigmented fungal species. Since overall oribatid mites preferred two 'Dematiacea' (*Alternaria alternata* and *Ulocladium* sp.), I conclude that niche differentiation in oribatid mites in respect to dark pigmented fungi is limited, but nevertheless may contribute to the high diversity of this microarthropod group.

Mycorrhizal fungi reach high densities in forest soils and are a potential food resource for oribatid mites. I investigated the feeding preferences of three oribatid mite species among six ectomycorrhizal and one ericoid mycorrhizal fungal species in a food choice experiment. Feeding preferences significantly differed between the oribatid mite species. However, overall, oribatid mites preferred two mycorrhizal species, *Hymenoscyphus ericae* and *Boletus badius*. This also supports the hypothesis that trophic niche differentiation in oribatid mites occurs, but appears not to be sufficient to solve the enigma of the large number of oribatid mite species in soil.

Trophic niche differentiation of 36 oribatid mite species/taxa from four forests was investigated using stable isotope analysis (^{15}N). The oribatid mite species investigated formed a gradient from phytophagous species over primary and secondary decomposer to

predators and scavengers (four trophic levels/feeding guilds). These surprisingly large differences in ^{15}N values of oribatid mite species strongly indicate that oribatid mites occupy different trophic niches in the field. This finding clearly supports the view that trophic niche differentiation is an important mechanism for the maintenance of the high number of oribatid mite species in forest ecosystems.

Intermediate disturbances may contribute to the coexistence of large numbers of plant and animal species. Therefore, I investigated the effect of three perturbation levels (single perturbation, perturbation once every two months and once every two weeks) on oribatid mite diversity and density in a field experiment. I hypothesised that the species number of oribatid mites is highest at the intermediate disturbance level (one perturbation every two month). In contrast to this hypothesis, oribatid mite diversity and density continually decreased with increasing perturbation level. These results suggest that the great majority of oribatid mite species are sensitive to disturbances irrespective of intensity and frequency. Therefore, the intermediate disturbance hypothesis presumably does not apply for oribatid mites.

The effect of the temporary enhancement of resources of different nutrients (wood, glucose & nitrogen & phosphorous (CNP), pet food, wheat bran) on oribatid mite diversity and density was investigated in a field experiment in the Solling (Germany). I hypothesised that the number and the density of oribatid mite species increase with the amount and quality of resources. The results of this experiment did not support this hypothesis, since the diversity of oribatid mites generally did not respond to the experimental treatments. The density of oribatid mites was slightly higher in the CNP-treatment compared to the pet food treatment. However, this increase likely resulted from indirect effects due to the decrease in earthworm density in the CNP-treatment. The results indicate that the oribatid mite community is not limited by the amount or quality of resources but rather by the burrowing and mixing activity of earthworms.

Overall, the results of the present study suggest that the coexistence of the large number of oribatid mites in soil cannot be explained by the presence of intermediate levels of disturbances or the amount and quality of resources but rather by the presence of trophic niche differentiation. The comparison of the results of the laboratory food choice experiments and the field study using stable isotopes indicate that oribatid mites feed on a wide range of substrates (when offered in the laboratory) but occupy rather distinct trophic niches in the field. To understand the factors that form these niches, further studies on the feeding biology of oribatid mites are necessary. In the future, recently established techniques such as the analysis of phospholipid fatty acids and the analysis of gut contents by molecular tools may contribute to the understanding of niche differentiation in oribatid mites.

CHAPTER 1 GENERAL INTRODUCTION

The aim of this study is to understand how the large number of soil living oribatid mites coexists in the rather uniform soil habitat (Anderson 1975a, Giller 1996). Usually, the diversity of animals and plants is explained via equilibrium or non-equilibrium dynamics. Since oribatid mite populations are rather stable it appears that there is no need to hypothesise non-equilibrium conditions where diversity is maintained by e.g. predation or disturbances (Paine 1966, Connell 1978). On the other hand, until now there is little evidence for niche differentiation on the major niche axes, such as food, time and space (Luxton 1972, Kaneko 1988, Siepel and de Ruiter-Dijkman 1993, Walter and Proctor 1999). Disentangling the reasons for these contradictory findings are the topic of this work.

Before discussing potential mechanisms that may contribute to the long-term maintenance of oribatid mite diversity I am introducing first the oribatid mites, second the fungi which are a potential food resource, third the interaction between these two groups of soil organisms and fourth the term diversity and the mechanisms which regulate local (α-) diversity. Afterwards, I explain how my work contribute to the understanding of the high α-diversity of soil living oribatid mites.

1.1. Oribatid mites

Oribatid mites (Oribatida, Acari) are mainly soil living decomposer microarthropods. They are a very old taxon; the first fossils of oribatid mites have been found in Devonian sediments (380 mya; Shear et al. 1984, Norton et al. 1988a, Kethley et al. 1989). One parthenogenetic species, *Muconothrus nasalis* (Trhypochthoniidae), is considered to be at least 200 million years old (Hammer and Wallwork 1979, Norton et al. 1988b).

Following the hypothesis of Grandjean (1969) oribatid mites consist of six morphologically distinct groups, the 'primitive' Palaeosomata, the species rich Enarthronota, the small group Parhypochthonioidea, the Mixonomata including the box mites, the species rich Desmonomata and the species rich Circumdehiscentiae (=Brachypylina, 'Higher Oribatida') that include five subgroups: Opsiopheredermata, Eupheredermata, dorsodeficient Apheredermata, pycnonotic Apheredermata and Poronota.

Until today it is not clear if oribatid mites are a monophyletic group. Some authors have proposed that Astigmata evolved within the oribatid mites, as a paedomorphic lineage (e.g. OConnor 1984, Norton 1998), however, molecular studies did not support this hypothesis (Maraun et al. 2004). Maraun et al. (2004) published the first phylogenetic tree of oribatid mites based on nucleotide sequences (Fig. 1.1.1.).

Oribatid mites consist of approximately 9,000 described species worldwide (Subias 2004) and the total species number is estimated to be up to 100,000 (Schatz 2002). In total 550 oribatid mite species occur in Germany (G. Weigmann, pers. comm.) and about 50-120 species are found in most forest ecosystems (Wunderle 1992). Oribatid mites are important decomposers in almost all habitats; their distribution ranges from arid coniferous forests over floodplain forests to salt marshes (Weigmann 1971, Usher 1975, Mitchell 1979). They reach the highest densities in forests, with higher densities in acid moder forests (up to 300,000 Ind/m²; Weigmann et al. 1989) than in calcareous mull forest (20,000 Ind/m²; Maraun and Scheu 2000).

Most oribatid mite species are K-selected (Norton 1994), they are usually small (mainly < 1 mm), they reproduce slowly (1-3 generations per year; Norton 1994), lay few eggs (1-6 per clutch) and they can become rather old (up to 3 years in Ptyctima; Travé et al. 1996). Several oribatid mite groups reproduce exclusively via parthenogenesis (*Nothrus*, Nanhermanniidae, Malaconothridae and Trhypochthoniidae).

Along with direct feeding on dead plant material and the resulting comminution of it, oribatid mites contribute to decomposition processes and nutrient cycling in the soil system by feeding on microorganisms and by the dispersal of microbial propagules (Behan and Hill 1978, Seastedt 1984, Moore et al. 1988, Maraun et al. 1998b; C. Renker, pers. comm.).

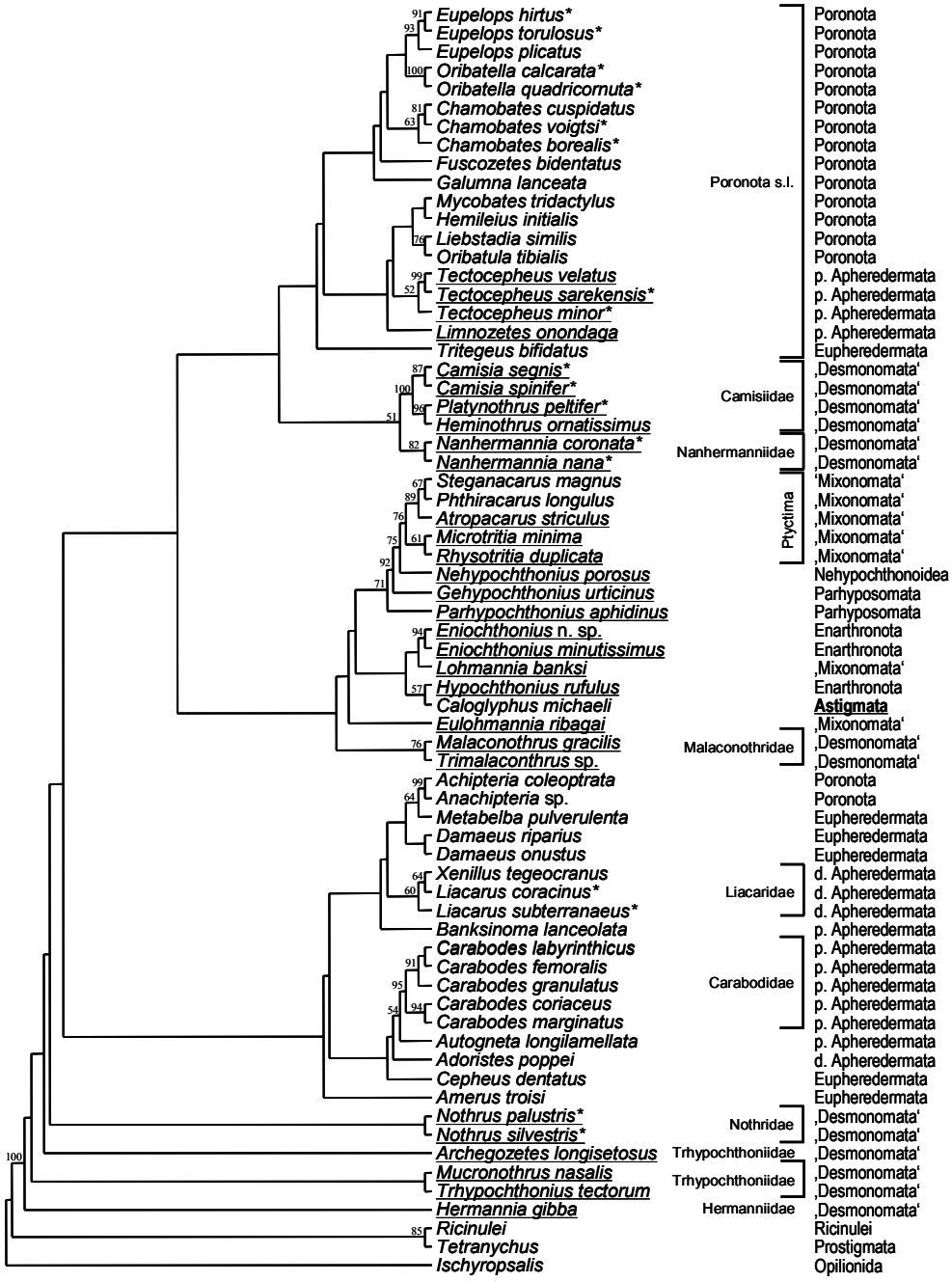

Fig. 1.1.1. Neighbour-joining tree of 64 species of oribatid mites, one astigmate mite and three outgroup taxa, constructed using the D3 region of the 28S rDNA. Number at nodes represent percentages of 1000 bootstrap replicates (only values above 50% were reported; Maraun et al. 2004).

1.2. Fungi

Fungi are eukaryotic organism, which comprise of about 1.5 million species (Hawksworth 1991, 2001). Within the fungi, five groups are separated: Chytridiomycota, Zygomycota, Basidiomycota, Ascomycota and Glomeromycota (Schüßler et al. 2001, Cracraft and Donoghue 2004,).

Fungi are heterotrophic, they absorb molecules by digesting with their filamentous tubes, termed hyphae, complex polymers, such as carbohydrates, lipids, proteins and nucleic acids. They release their digestive enzymes into the surrounding and absorb the available nutrients (external rumen; Swift et al. 1979). Saprophytic fungi are able to degrade cellulose and lignin (Domsch and Gams 1969, Dix and Webster 1995) which enables them to decompose litter and wood. Anderson and Domsch (1975) showed that fungal metabolic activity accounts for more than half of the carbon mineralization in forest soils.

Along with decomposition, fungi have several important functions in the ecosystems, such as symbiosis and parasitism. Symbioses are widespread, e.g. lichens, mycorrhiza and endophytes of plants. One-fourth of all described fungal species form lichens and almost all plant species are associated with mycorrhizal fungi (Smith and Read 1997). Additionally, there are symbioses with animals, such as ants and other insects (Borkott and Insam 1990, Suh et al. 2003). In contrast to the parasitic character of some fungi (Lehmann 1985, Roncero et al. 2003), *Penicillium* is the producer of the most common life-saving antibiotic penicillin.

1.3. Interactions between microarthropods and fungi

Interactions between microarthropods and fungi are central to many processes in soil, such as decomposition and nutrient cycling (Lussenhop 1992, Bonkowski et al. 2000, Cortet et al. 2003). Surprisingly, the possible mechanisms of these interactions, such as grazing,

disturbance and dispersal, have been little studied. Grazing of soil animals on fungi may affect the competition between saprophytic and mycorrhizal fungi (Tiunov and Scheu 2005), the recovery and succession of saprophytic fungi (Visser 1985, Maraun et al. 1998b), and the dispersal of fungal propagules (Anderson 1988, Renker et al. 2005).

In the rhizosphere, microarthropods affect saprophytic and pathogenic fungi, as well as vesicular-arbuscular and ectomycorrhizal fungi via selective grazing and dispersal (Lussenhop 1992). For example, collembolan feeding on mycorrhizal hyphae reduces the mycorrhizal benefits for the plants (Warnock et al. 1982, Finlay 1985). In contrast to Collembola and other microarthropods, the interactions of oribatid mites with rhizosphere fungi are little studied (see Klironomos and Kendrick 1995, 1996).

1.4. Diversity

The measurement of species diversity includes the number and relative abundance of species within a community. Species diversity can be measured as local (α-) and regional (γ-) diversity (MacArthur 1965, Whittaker 1972). Alpha-diversity is the number of species in a more or less uniform habitat, which is a result of competition, predation and other interspecific interactions at the local community level. Gamma-diversity is the total number of species occurring in all habitats within a region (= geographic area that includes no significant barriers to dispersal of organisms), which is determined by evolutionary processes, such as species production, migration and historical occasions of geographic location. The difference in species from one habitat to the next is called β-diversity (species turnover), which is the ratio of γ-diversity to α-diversity (β-diversity = γ-diversity/α-diversity). Higher γ-diversity suggests higher habitat specialization.

In forest soils the α-diversity of the macrofauna usually is low (e.g. earthworms: 3-6 species per site, Edwards and Bohlen 1996; diplopods: 3-10 species per site, isopods: 1-5 species per site; Scheu and Schulz 1996) whereas the α-diversity of soil microarthropods,

such as collembolans (average of about 40-50 species per site, Hopkin 1997) and oribatid mites (average of 50-70 species per site, Luxton 1975, Persson et al. 1980), is high. The high α-diversity of decomposer animals in soil is one of the great enigmas of soil biology (Anderson 1975a, Giller 1996, Maraun et al. 2003a). Due to the high diversity of soil invertebrates soils have been termed 'the poor man's tropical rainforest' (Usher et al. 1979).

1.4.1. The niche concept

According to the fundamental niche concept (Hutchinson 1957) the niche space is defined as an n-dimensional space (hypervolume) which comprises dimensions such as space, time, temperature and resources. This concept predicts that the number of species in an ecosystem depends on the number of niches available and on the niche breadth of each species. An overlap of niche use of the species is limited since a strong niche overlap would result in competitive exclusion (Chesson and Case 1986). Hutchinson (1959) argued that competition is the major process controlling animal and plant community structure. In most communities, competition for space and nutrients occurs (Yodzis 1986). Gause (1934) stated "as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each take possession of certain peculiar kinds of food and modes of life in which it has an advantage over its competitor" (competitive exclusion). The partitioning of resources and the resulting niche differentiation is one way to allow the coexistence of large numbers of species.

1.4.2. Regulatory factors of α-diversity

During the last century, a number of hypothesis have been developed that contributed to our understanding of animal and plant diversity. Factors which regulate diversity are e.g. history, habitat heterogeneity, competition, predation, productivity and disturbance. These

factors depend on the nature of the community, i.e. if it is an equilibrium or a non-equilibrium community. Communities are in equilibrium conditions when species diversity, abundances and composition remain constant over time (Krebs 2001). Equilibrium communities are in a 'state of balance', which means that invasions are limited, the community has high resilience, resistance and persistence and is saturated in species number. These communities are regulated by biotic interactions, such as competition and predation, which operate in a density-dependent manner (Hutchinson 1959, Levin 1974, Chesson and Case 1986). Non-equilibrium communities are patchy and regulated by density independent factors such as disturbances (e.g. fires, hurricanes, flooding, grazing, predation, pest) and underlie lottery dynamics (Hanski 1991, Huston 1994). They occur when disturbance intervals are shorter than recovery times, so that the community never reach equilibrium. Therefore, the structure of such communities might be unpredictable (Giller 1996). Coral reefs are typical non-equilibrium communities because they are driven by the lottery of variable recruitment (Sale 1977, 1987, Connell 1978, 1987).

There are only few studies which studied whether the microarthropod community in soil is in an equilibrium or in a non-equilibrium state. Kampichler and Geissen (2005) investigated the temporal predictability of soil microarthropod communities in temperate forests. They concluded that density-dependent dynamics tend to stabilize time series of Collembola and prevent directional change of community composition. Additionally, Maraun and Scheu (2000) found that the community structure of oribatid mites is predictable for different forest types. Oribatid mites also tend to have stable populations (Norton 1985) and, therefore, there is little evidence for non-equilibrium dynamics.

1.5. Factors regulating oribatid mite diversity and objectives of this study

The following paragraphs outline patterns of oribatid mite diversity such as trophic niche differentiation, disturbance and resource availability, and highlight my contribution to the understanding of oribatid mite diversity.

Trophic niche differention may lead to reduced competition between species and may therefore explain the high diversity of soil animal species (Anderson 1975a). Soil animals tend to be food generalists (Giller 1996) due to their close spatial association (Scheu and Setälä 2002). Investigations on the feeding biology of oribatid mites, including gut content analysis and analyses of enzyme activities, indicate that most oribatid mite species ingest a wide range of food materials (Luxton 1972, Behan-Pelletier and Hill 1983, Siepel and de Ruiter-Dijkman 1993). In contrast, results of food choice experiments suggest that oribatid mites preferentially feed on certain fungal species (Mitchell and Parkinson 1976, Kaneko et al. 1995) and that dark pigmented fungi are preferred over hyaline fungi (Maraun et al. 1998a). However, until now it has never been investigated if there is trophic niche differentiation concerning dark pigmented fungi, i.e. if there are species specific feeding preferences for 'Dematiacea'. Therefore, I investigated the feeding preferences of oribatid mites among different species of dark pigmented fungi ('Dematiacea') which could indicate trophic niche differentiation in oribatid mites (**CHAPTER 2.1.**).

Mycorrhizal fungi are a potential food resource for soil microarthropods (Lussenhop 1992, Gunn and Cherrett 1993, Larsen and Jakobson 1996, Hopkin 1997). Collembolan grazing on mycorrhizal fungi and the resulting effect on plant growth is well studied (Klironomos and Kendrick 1995, 1996, Klironomos and Moutoglis 1999). In addition, Hiol Hiol et al. (1994) and Shaw (1985) showed that ectomycorrhizal fungi are consumed by Collembola species. Until now the feeding preferences of oribatid mites for ectomycorrhizal fungi have not been studied and, consequently, the potential of trophic niche differentiation has never been evaluated. Therefore, I investigated oribatid mite

feeding on ectomycorrhizal fungi in a laboratory food choice experiment. Different feeding preferences among ectomycorrhizal fungi would result in partitioning of this resource and may lead to reduced competition between oribatid mite species (**CHAPTER 2.2.**).

Stable isotope analyses are increasingly used to investigate the trophic levels and the trophic niche differentiation in animal communities (Minagawa and Wada 1984, Wada et al. 1991, Ponsard and Arditi 2000, Post 2002, McCutchan et al. 2003). Surprisingly, few studies used this method to investigate the trophic structure of the soil food web (Ponsard and Arditi 2000, Scheu and Falca 2000). Scheu and Falca (2000) for the first time included oribatid mite species in their investigation on the food web structure of two different beech forests. Their findings indicate that oribatid mite species belong to the primary and secondary decomposer group, which feed predominantly litter and fungi, respectively. Due to the fact that only a small number of oribatid mite species was investigated (eight large species) and no putative predators or scavengers were included in that study, I carried out a more comprehensive study on the trophic position, i.e. the trophic niche differentiation, using 36 species/taxa of oribatid mites from four different temperate forests (**CHAPTER 2.3.**).

Disturbance may be one of the main factors which prevents species from competitive exclusion in non-equilibrium communities (DeAngelis and Waterhouse 1987, Huston 1994). Abiotic fluctuations, predation and herbivory function as disturbances and can result in a patchy habitat that undergoes succession, which allows the coexistence of a number of species (Connell 1987). Disturbances can be predictable and unpredictable, and therefore species can be differentially affected, depending on their life-history. K-selected species, such as oribatid mites, are likely to be more affected by unpredictable disturbances. The intermediate disturbance hypothesis (Grime 1973, Horn 1975, Connell 1978) predicts that intermediate degrees of disturbances reduce the intensity of competition between species and hence the competitive exclusion of species. Huston (1979, 1994)

extended this hypothesis by including the growth rate of the population. His 'dynamic equilibrium model' or 'patch dynamic system' deals with the interaction between the extent of disturbances in the community and the rate of population growth of the species in the community. The highest level of diversity occurs at sites where the intensity and the growth rate are similar. There are only few studies which investigated the influence of disturbances on the diversity of oribatid mites (Scheu und Schulz 1996, Siepel 1996, Maraun et al. 1999, 2001). Results of these studies suggest that earthworm activity could act as a severe disturbance for microarthropods. To study the effect of different levels of disturbances on oribatid mite diversity, density and community structure, I simulated the effect of different intensities of earthworm activity on oribatid mites in a beech forest (**CHAPTER 2.4.**).

High productivity or resource availability in a relatively stable environment has been assumed to result in greater species diversity (productivity-stability hypothesis; Connell and Orias 1964, Whittaker and Niering 1965, Tilman 1982). However, investigations on this topic resulted in controversial findings. Some studies documented a positive correlation between productivity and diversity (e.g. Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Wright et al. 1993) whereas others found no correlation or even a negative one (Tilman 1986, Currie 1991). The negative relationship between productivity and species number has been termed the 'paradox of enrichment' (Riebesell 1974, Rosenzweig 1975). Soil decomposer animals in general appear to be limited by resources, i.e. are bottom-up controlled, since litter does not accumulate (Hairston et al. 1960, Scheu and Schaefer 1998, Ponsard et al. 2000). However, this resource limitation is only true for soil macroarthropds and other soil animals that feed directly on the litter material. Soil microarthropods may not be limited by the amount of resources since they do not feed on the litter material but on fungi. However, the importance of resource limitation for oribatid mite diversity has hardly been studied until now. Maraun et al.

(2001) found that the effect of resource addition for microarthropods is superimposed by indirect effects, such as increased earthworm activity. However, the fact that the experiment was carried out in a forest rich in earthworms (Göttinger forest) and the earthworms benefited from the added resources hampered the interpretation of the response of microarthropods. Therefore, I investigated the effect of resource addition and resource quality on the oribatid mite community in an acidic forest where earthworm densities are low (Solling; **CHAPTER 2.5.**).

CHAPTER 2 UNDERSTANDING ORIBATID MITE DIVERSITY

2.1. Feeding preferences among dark pigmented fungal taxa ('Dematiacea') indicate limited trophic niche differentiation of oribatid mites (Oribatida, Acari)

2.1.1. Abstract

Trophic niche differentiation may explain the high diversity of soil animal species. However, trophic niches of soil invertebrate species are little understood and it appears that different decomposer soil animal species prefer similar food substrates. Soil microarthropods, such as collembolans and oribatid mites, preferentially feed on dark pigmented fungi ('Dematiacea') but their feeding preferences among different dark pigmented fungal species are little studied. In this study I offered eight dark pigmented fungal taxa (*Alternaria alternata*, *Bipolaris spicifera*, *Chloridium* sp., *Cladosporium* sp., *Codinea* sp., *Oidiodendron* sp., *Phialophora verrucosa*, *Ulocladium* sp.) and two little pigmented fungal species (*Aureobasidium pullulans* and *Mortierella ramanniana*) to 10 species of oribatid mites. Despite the overall trend of oribatid mites to prefer two of the dark pigmented fungi (*Alternaria alternata* and *Ulocladium* sp.), feeding preferences significantly differed between the oribatid mite species. *Achipteria coleoptrata*, *Carabodes* sp., *Liacarus subterraneus*, *Oribatella quadricornuta* and *Steganacarus magnus* strongly preferred *Alternaria alternata* and *Ulocladium* sp.; *Hypochthonius rufulus* preferred *Phialophora verrucosa*. Species with low feeding preferences, *Eupelops torulosus* and *Oribatula tibialis,* preferentially fed on *Ulocladium* sp. and *Codinea* sp., respectively. The other species (*Nothrus silvestris*, *Platynothrus peltifer*) had no clear feeding preferences. The results support the view that trophic niche differentiation in oribatid mite species is limited, but may contribute to the high diversity of soil animal species.

2.1.2. Introduction

Oribatid mites are among the most abundant and diverse microarthropods in forest soils. Their densities in forest floors of the temperate region range between 20,000 and 400,000 ind m^{-2} with a high alpha diversity but a low beta diversity (Maraun and Scheu 2000). The high diversity of oribatid mites (60 to 120 species per site), and decomposer soil animals in general, is one of the great riddles in soil ecology (Anderson 1975a, Schaefer 1991). Anderson (1975a) proposed three hypotheses to explain soil animal species diversity: (1) food for soil animals is available in excess and therefore competition for food is limited, (2) species are separated by colonizing different microhabitats or (3) species use different food resources. There is no evidence supporting the first hypothesis rather, theoretical and experimental evidence suggest that food resources in soil are of limited supply (Slobodkin et al. 1967, Scheu and Schaefer 1998).

Oribatid mites live in very different microhabitats, e.g. in the litter layer, the humus layer, in dead wood, in moss and in the bark of trees, and this contributes to the high diversity of oribatid mites (Aoki 1967, Hammer 1972, Wunderle 1992, Hansen 2000). Furthermore, Anderson (1973) has shown that the litter layer in mixed deciduous woodland forms a mosaic of microhabitats in time and space and this may allow more species to coexist. From the perspective of minute soil invertebrates one layer of the soil profile consists of a large number of "compartments" each consisting of a range of different habitats.

Food specialization remains a key issue for understanding animal species diversity in soil. Even small differences in food preferences of oribatid mites may reduce competition between species. Surprisingly, knowledge on feeding biology of many soil invertebrates is poor and the available information in part is contradictory. Gut content analyses and analyses of enzyme activity indicate that most oribatid mites ingest a wide range of food materials including spores and hyphae of various fungal species, plant material, conifer

pollen and parts of animal bodies (Luxton 1972, Behan-Pelletier and Hill 1983, Siepel and de Ruiter-Dijkman 1993). In contrast, food choice experiments suggest that oribatid mites preferentially feed on fungal species (Mitchell and Parkinson 1976, Kaneko et al. 1995, Maraun et al. 1998a). Recent studies on the natural variation in stable isotope ratios ($^{15}N/^{14}N$) indicate that oribatid mites use very different food resources ranging from plant material to animal tissue (Schneider et al. 2004).

More detailed knowledge on the feeding biology of oribatid mites is necessary for understanding niche differentiation between species but it is also important for understanding the effect of oribatid mites on the community structure of fungi in soil. Grazing on fungi by oribatid mites has been found to affect the fungal community in some studies (Maraun et al. 1998b) but not in others (McLean et al. 1996). Furthermore, knowledge on the feeding biology of oribatid mites is important to understand to what extent soil microarthropods are limited by the availability of food resources (bottom-up control). Additionally, understanding co-evolutionary interactions between soil fungi and soil microarthropods may contribute to uncover the forces which were responsible for the evolution of the high number of oribatid mite species (Bernini 1986, Norton et al. 1993, Maraun et al. 2003a).

This study adds to previous investigations on food preferences of oribatid mites by investigating different species of dark pigmented fungi since little is known on food preferences of oribatid mite species for different dark pigmented fungal taxa. I hypothesize that selective feeding by oribatid mite species on different species of 'Dematiacea' contributes to the high diversity of oribatid mites.

2.1.3. Materials and Methods

Experimental design and sampling

In Mai 2002 oribatid mites were extracted by heat (Kempson et al. 1963) from the soil of a beech-oak forest near Darmstadt (Kranichsteiner Wald, Hesse, Germany). The following 10 oribatid mite species colonising the litter layer were collected: *Achipteria coleoptrata*, *Carabodes* sp., *Eupelops torulosus*, *Hypochthonius rufulus*, *Liacarus subterraneus*, *Nothrus silvestris*, *Oribatella quadricornuta*, *Oribatula tibialis*, *Platynothrus peltifer* and *Steganacarus magnus*.

Ten fungal species were offered as food substrates simultaneously to single species of oribatid mites: *Alternaria alternata*, *Bipolaris spicifera*, *Chloridium* sp., *Cladosporium* sp., *Codinea* sp., *Oidiodendron* sp., *Phialophora verrucosa*, *Ulocladium* sp. (all 'Dematiacea'), *Mortierella ramanniana* (Zygomycetes) and *Aureobasidium pullulans* (Moniliales). The fungal species were extracted from leaf litter material (beech-oak) of the Kranichstein forest near Darmstadt (Germany). They were stored in the laboratory until the beginning of the experiment. Two weeks before the start of the experiment they were freshly inoculated on malt extract agar (2%). Species names of the fungi are subsequently abbreviated as genera names.

The fungi were offered on small agar discs (8 mm Ø) which were cut out of the growing front of the fungal colonies and placed in a circle of 5 cm in a plastic vessel (7 cm Ø). The bottom of the vessels consisted of a layer of plaster of Paris. Twenty oribatid mites of the respective species were placed in the centre of the vessels. After 10 days faecal pellets deposited in close vicinity of the fungal agar discs were counted and taken as a measure of the amount of food consumed. There were five replicates per treatment. During the course of the experiment none of the fungal isolates became contaminated with other fungi.

Statistical analysis

For statistical analysis the number of faecal pellets was log-transformed to increase homogeneity of variance. The feeding preferences of all oribatid mites were analysed by single factor analysis of variance (ANOVA) with the factors 'fungi' (ten fungal species). For comparison of means Tukey's honestly significant difference (HSD) was calculated (Sokal and Rohlf 1995). The food choice (number of faecal pellets) of the respective oribatid mites was analysed by one-way multivariate analysis of variance (MANOVA, Pillai's Trace; Scheiner and Gurevitch 2001) with the factor 'fungi' with 10 levels (the 10 fungal species). Subsequently, protected ANOVAs (Scheiner and Gurevitch 2001) were performed to locate which of the oribatid mite species contributed to significant MANOVA results. The analyses were implemented in SAS 8e (SAS Institute Inc., Cary, USA).

2.1.4. Results

Feeding of the oribatid mites on the ten offered fungal species significantly differed between the mite species ($F_{9,490} = 12.19$; $P < 0.0001$). Overall, *Alternaria* was most preferred as indicated by the high number of pellets deposited (Fig. 2.1.1.). The other fungal taxa were also ingested with *Ulocladium* being the second preferred species, *Phialophora, Aureobasidium, Codinea, Cladosporium* being of intermediate preference and *Oidiodendron, Mortierella, Bipolaris, Chloridium* being least preferred. The non-'Dematiacea' (*Aureobasidium* and *Mortierella*) ranked among the species of intermediate or low preference.

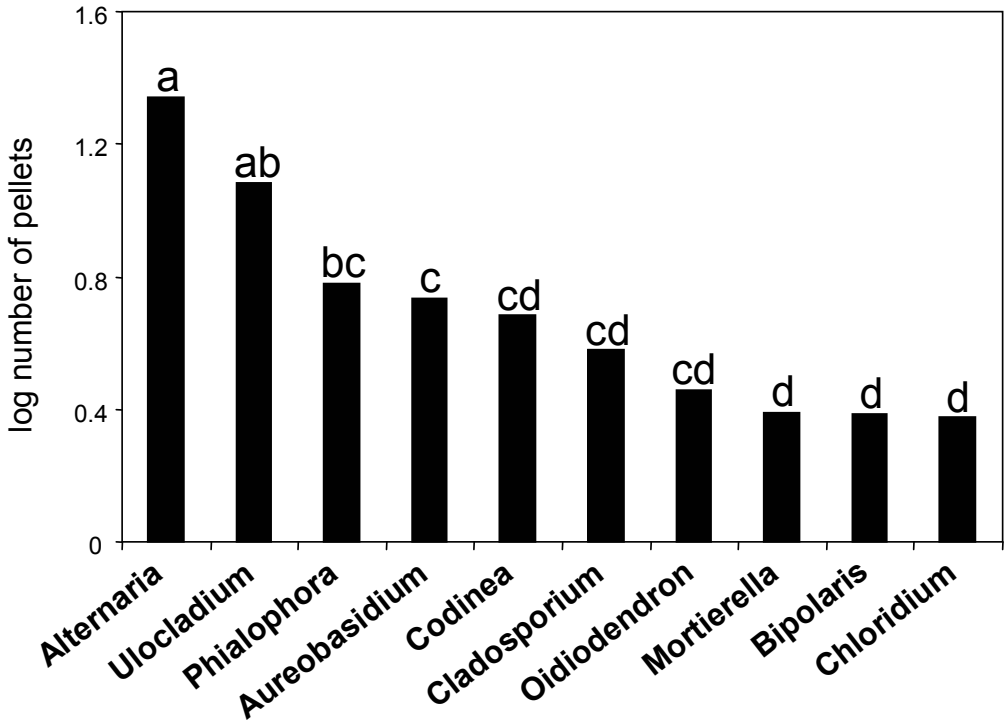

Fig. 2.1.1. Total Number of faecal pellets from all individuals of the 10 investigated oribatid mite species deposited close to each investigated fungus (*Alternaria alternata*, *Bipolaris spicifera*, *Chloridium* sp., *Cladosporium* sp., *Codinea* sp., *Oidiodendron* sp., *Phialophora verrucosa*, *Ulocladium* sp., *Mortierella ramanniana* and *Aureobasidium pullulans*) during 10 days of incubation. Fungi were offered simultaneously. Log-transformed data; bars with different letters are significantly different.

Feeding preferences of oribatid mites significantly differed between species (see MANOVA, Table 2.1.1.). As indicated by protected ANOVAs feeding preferences were strong in *A. coleoptrata*, *Carabodes* sp., *H. rufulus*, *L. subterraneus*, *O. quadricornuta* and *S. magnus*, low in *E. torulosus* and *O. tibialis*, and not significant in *P. peltifer* and *N. silvestris* (Table 2.1.1.). Species with strong feeding preferences generally preferred *Alternaria* and *Ulocladium* except *H. rufulus*, which preferentially fed on *Phialophora* (Fig. 2.1.2.). Oribatid mite species with low feeding preferences, *E. torulosus* and *O. tibialis*, preferentially fed on *Ulocladium* and *Codinea*, respectively (Fig. 2.1.2.).

Table 2.1.1. MANOVA (Pillai's trace) table of F values on variations in the number of faecal pellets (log-transformed data) produced by oribatid mites feeding on ten different fungal taxa offered as food substrate, and F-values of protected ANOVAs on variations in the number of faecal pellets deposited by each oribatid mite species (log-transformed data).

	df	*F values*
MANOVA:		
Pillai's Trace	90,351	2.23 ***
Protected ANOVA:		
Achipteria coleoptrata	9,49	10.84 ***
Carabodes sp.	9,49	7.55 ***
Hypochthonius rufulus	9,49	6.30 ***
Liacarus subterraneus	9,49	4.88 ***
Oribatella quadrincornuta	9,49	4.70 ***
Steganacarus magnus	9,49	4.54 ***
Eupelops torulosus	9,49	2.37 *
Oribatula tibialis	9,49	2.27 *
Platynothrus peltifer	9,49	1.51
Nothrus silvestris	9,49	1.45

**P < 0.05, ***P < 0.001, df = degrees of freedom*

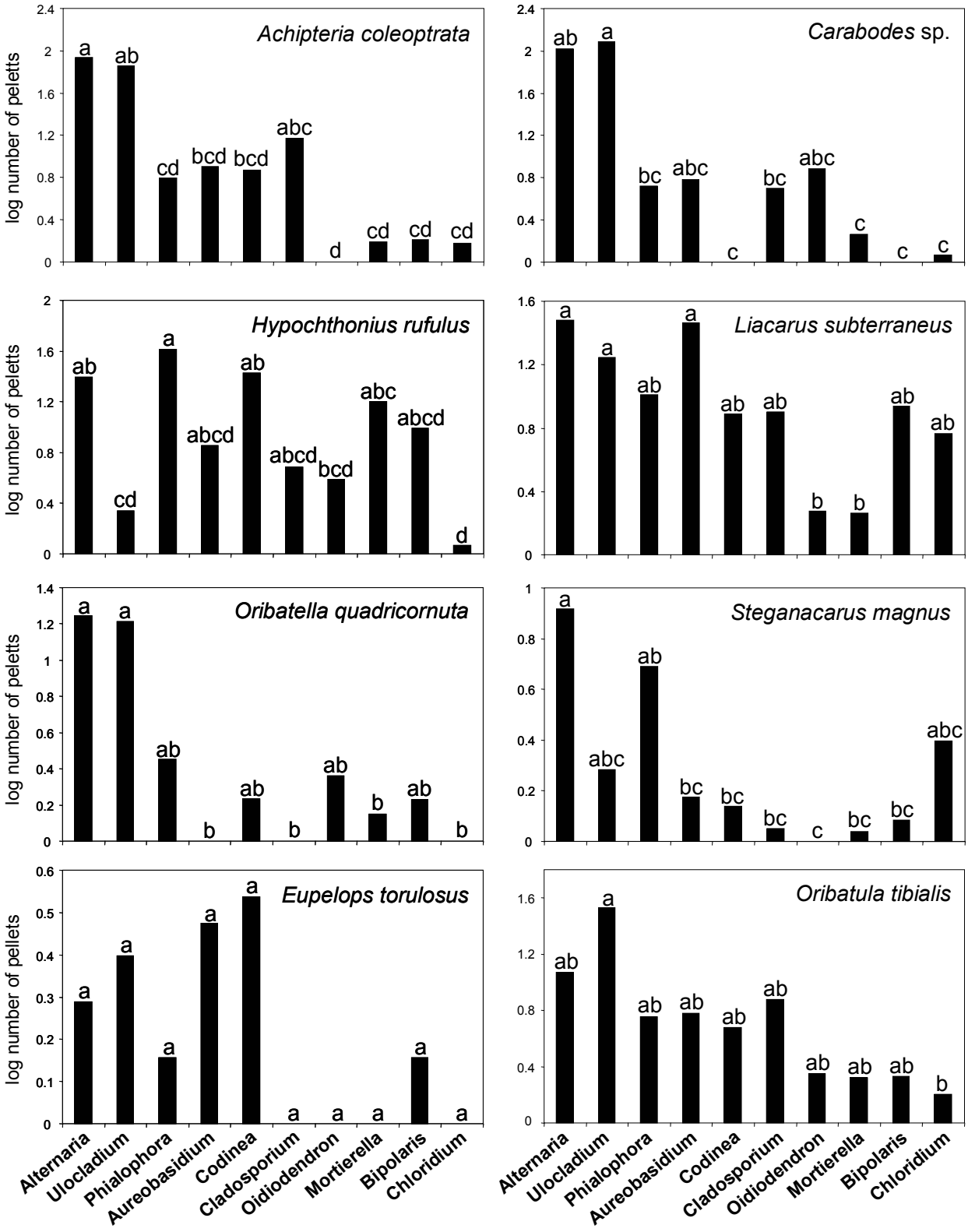

Fig. 2.1.2. Number of faecal pellets produced by different species of oribatid mites during 10 days of incubation (log-transformed data; bars showing the same letter are not significantly different, Tukey's studentized range test, $P < 0.05$). Note the different scales.

2.1.5. Discussion

Oribatid mites are specious soil invertebrates. Their high diversity is surprising considering the relative uniformity of the environment (litter and soil) and of major food resources (detritus; Anderson and Healey 1972). Explanations for high species diversity have traditionally been based on equilibrium concepts stressing that niche partitioning is strong (Giller 1996). The present study addressed two contradictory observations. On one side soil animals, especially oribatid mites, appear to feed on a wide range of food substrates (Behan-Pelletier and Hill 1983, Scheu and Setälä 2002) supporting the view that most soil animals are generalist feeders (Maraun et al. 2003a). On the other side there is evidence for niche differentiation (Anderson 1975b, 1978) and stable isotope ratios on natural variation in $^{15}N/^{14}N$ suggest that oribatid mite species use different food resources (Scheu and Falca 2000). Recently, it has been shown that natural variations in $^{15}N/^{14}N$ ratios in oribatid mite species span over a range of 12 delta units which is equivalent to three to four trophic levels (Schneider et al. 2004). Furthermore, it has been shown that oribatid mites preferentially feed on dark pigmented fungi ('Dematiacea') and tend to reject hyaline forms suggesting food specialization (Maraun et al. 1998a). In this study I investigated whether food preferences of oribatid mite species differ among dark pigmented fungal species. Selective feeding of oribatid mites (and other soil animals) on certain dark pigmented fungal species may help explaining the high diversity of oribatid mite species and also understanding to what extent oribatid mites affect the structure and functioning of the fungal community in soil (Behan-Pelletier and Hill 1983, Visser 1985, McLean et al. 1996, Maraun et al. 1998b). Additionally, feeding of soil microarthropods on certain dark pigmented fungi may help understanding which factors control the species composition and density of oribatid mites in the field.

Results of the present study support our hypothesis that food preferences of oribatid mite species for dark pigmented fungi differ. However, differences in food preferences

between oribatid mite species in part were small. Most species preferentially fed on dark pigmented fungi, such as *Alternaria* and *Ulocladium*, which is consistent with previous findings. *Oribatella quadricornuta* is known to feed on fungi in particular on dark pigmented species (Schuster 1956, Siepel and de Ruiter-Dijkmann 1993). *Steganacarus magnus* is known to preferentially feed on *Alternaria*, *Phialophora* and *Cladosporium* (Maraun et al. 1998a). By contrast, Schneider et al. (2004) ascribed *S. magnus* to primary decomposers and Siepel and de Ruiter-Dijkman (1993) concluded that this species feeds on litter material little colonized by fungi. *Carabodes* sp. and *A. coleoptrata* preferentially fed on *Alternaria* and *Ulocladium* in this study whereas stable isotope data (^{15}N) suggest that they predominantly feed on litter (Schneider et al. 2004). Schuster (1956) ascribed *A. coleoptrata* and *Carabodes femoralis* to microphytophages, feeding on fungi, pollen, moos, algae and lichens. *Hypochthonius rufulus* showed clear feeding preferences in this study. In contrast, Maraun et al. (1998a) found *H. rufulus* to feed on a wide variety of fungi, Siepel and de Ruiter-Dijkman (1993) ascribed it to omnivores, Riha (1951) observed it feeding on carcasses of collembolans and worms, and Schneider et al. (2004) ascribed *H. rufulus* to omnivores.

Oribatula tibialis and *E. torulosus* preferentially fed on *Ulocladium*, *Aureobasidium* and *Codinea*. Siepel and de Ruiter-Dijkman (1993) concluded these species to feed on fungi and Schneider et al. (2004) ascribed *Eupelops* (*E. plicatus*) and other Oribatuloidea to secondary decomposers.

Indiscriminate feeding on fungal species by *P. peltifer* and *N. silvestris* in this study is consistent with results of Schuster (1956), who also assumed these species to be little specialized. Both species are known to feed on litter (Siepel and de Ruiter-Dijkman 1993), and this is also reflected in stable isotope (^{15}N) data (Schneider et al. 2004).

In conclusion, most oribatid mite species appear to preferentially feed on certain species of dark pigmented fungi, such as *Alternaria* and *Ulocladium*, but the food spectrum varies

among oribatid mite species suggesting that partitioning of food resources may contribute to the coexistence of oribatid mite species. However, differences in food preferences between oribatid mite species are rather small and therefore are insufficient to explain the high species diversity of oribatid mites. Other factors, such as temporal and spatial niche partitioning may be responsible for differential use of food resources and explain the very different $^{15}N/^{14}N$ ratios in oribatid mites as documented by Schneider et al. (2004). Overall, findings of the present study indicate that oribatid mite species generally feed on a wide spectrum of fungal species. Despite preferences for certain fungal species most oribatid mites are best considered "choosy generalists".

2.2. Oribatid mite (Oribatida, Acari) feeding on ectomycorrhizal fungi

2.2.1. Abstarct

The coexistence of a large number of soil animals without extensive niche differentiation is one of the great riddles in soil biology. The main aim of this study was to explore the importance of partitioning of food resources for the high diversity of microarthropods in soil. In addition, I investigated if ectomycorrhizal fungi are preferrentially consumed compared to saprotrophic fungi. Until today, ectomycorrhizal fungi have never been tested as potential food resource for oribatid mites. I offered six ectomycorrhizal fungi (*Amanita muscaria* (L.) Hook., *Boletus badius* (Fr.) Fr., *Cenococcum geophilum* Fr., *Laccaria laccata* (Scop.) Fr., *Paxillus involutus* (Batsch) Fr., *Piloderma croceum* J. Erikss. & Hjortstam), one ericoid mycorrhizal fungus (*Hymenoscyphus ericae* (D.J. Read) Korf & Kernan) and three saprotrophic fungi (*Agrocybe gibberosa* (Fr.) Fayod, *Alternaria alternata* (Fr.) Keissl., *Mortierella ramanniana* (A. Møller) Linnem.) simultaneously to each of the mainly mycophagous oribatid mite species *Carabodes femoralis* (Nicolet), *Nothrus silvestris* Nicolet and *Oribatula tibialis* Nicolet. The ericoid mycorrhizal fungus *Hymenoscyphus ericae* and the ectomycorrhizal fungus *Boletus badius* were preferentially consumed by each oribatid mite species. However, feeding preferences differed significantly between the three species, with *Oribatula tibialis* being most selective. This study for the first time documented that oribatid mites feed on certain ectomycorrhizal fungi, which may contribute to the diversity of this group. The relevance of feeding of oribatid mites on ectomycorrhizal fungi for plant performance is discussed.

2.2.2. Introduction

Microarthropods are among the most abundant decomposers in soil. Oribatid mites (Acari, Oribatida), as part of the microarthropod community, reach densities of up to 400,000 ind/m² in temperate forests. They comprise about 10,000 described species worldwide (Schatz 2002), of which 550 occur in Germany (G. Weigmann, pers. comm.). Wunderle (1992) found 119 oribatid mite species in a temperate beech forest in Germany. Surprisingly, it is still unknown how this large number of species can coexist without extensive niche differentiation (Anderson 1975a).

Limited evidence for trophic niche differentiation has been found in studies on gut content, cheliceral size and enzyme activity in the gut of oribatid mites (Schuster 1956, Luxton 1972, Kaneko 1988, Siepel and de Ruiter-Dijkman 1993). In contrast, Schneider et al. (2004) documented strong trophic niche differentiation in oribatid mites using stable istopes (^{15}N). However, food choice experiments indicated a general preference for dark pigmented fungi ('Dematiacea'; Maraun et al. 1998a). Therefore, Schneider and Maraun (2005) coined the term 'choosy generalists' for oribatid mites since they generally have a wide food spectrum but feed selectively when high quality food is available.

Fungal grazing by microarthropods affects microbial respiration (Bengtsson and Rundgren 1983, Kaneko et al. 1998), decomposition rates (Cortet et al. 2003), nutrient cycling (Bonkowski et al. 2000), plant growth (Klironomos and Kendrick 1995), fungal biomass (Hanlon and Anderson 1979, Bardgett et al. 1993), fungal succession (Visser 1985), the distribution of fungi in soils (Lussenhop 1992) and the interaction between competing fungal species (Tiunov and Scheu 2005). While grazing on saprotrophic fungi and arbuscular mycorrhizal (AM) fungi is well studied (Lussenhop 1992, Gunn and Cherrett 1993, Larsen and Jakobsen 1996, Hopkin 1997, Klironomos and Moutoglis 1999, Sabatini and Innocenti 2000, Cole et al. 2004) the feeding on ectomycorrhizal fungi has hardly been investigated. This is surprising since ectomycorrhizal fungi are common in

soils (Read et al. 1992) and are probably of high nutritional value (Wolters 1985, Schultz 1991, Hopkin 1997). Furthermore, the interaction between soil microarthropods and ectomycorrhizal fungi may affect plant performance (Smith and Read 1997).

More often than oribatid mites collembolans have been used to study effects of soil microarthropods on mycorrhizal fungi. *Proisotoma minuta* and *Onychiurus armatus* consumed a number of ectomycorrhizal fungi offered in laboratory food choice experiments (Shaw 1985, 1988, Hiol Hiol et al. 1994). Klironomos and Kendrick (1996) investigated the feeding preferences of six species of mites and collembolans for one AM fungus and two saprotrophic fungi and showed that they preferentially graze on hyphae of conidial fungi rather than on those of AM fungi. However, oribatid mite feeding on ectomycorrhizal fungi has never been studied.

This study for the first time investigates feeding preferences of oribatid mites for ectomycorrhizal fungi. Feeding preferences for ectomycorrhizal fungal species were compared with those for saprotrophic fungi. I hypothesized that oribatid mite species selectively feed on ectomycorrhizal fungi, which may partially explain how the large number of oribatid mite species can coexist.

2.2.3. Materials and Methods

Experimental design and sampling

In April 2004 the oribatid mite species *Carabodes femoralis* (Nicolet), *Nothrus silvestris* Nicolet and *Oribatula tibialis* Nicolet were extracted by heat (Kempson et al. 1963) from the soil of a beech-oak forest near Darmstadt (Kranichsteiner Wald, Hesse, Germany). I chose these oribatid mite species because they mainly feed on fungi (Schneider et al. 2004).

Six ectomycorrhizal fungi, *Amanita muscaria* (L.) Hook., *Boletus badius* (Fr.) Fr., *Cenococcum geophilum* Fr., *Laccaria laccata* (Scop.) Fr., *Paxillus involutus* (Batsch) Fr.,

Piloderma croceum J. Erikss. & Hjortstam, one ericoid mycorrhizal fungus *Hymenoscyphus ericae* (D.J. Read) Korf & Kernan and three saprotrophic fungi, *Agrocybe gibberosa* (Fr.) Fayod, *Alternaria alternata* (Fr.) Keissl., *Mortierella ramanniana* (A. Møller) Linnem. (Table 1) were offered simultaneously to each oribatid mite species. The three saprotrophic fungal species were chosen because they ranked from high to low food quality (*Alternaria alternata*: high, *Mortierella ramanniana*: intermediate, *Agrocybe gibberosa*: low; Ruess et al. 2000, Maraun et al. 2003a, Schneider and Maraun 2005), and because I wanted to compare feeding preferences of oribatid mites on ectomycorrhiza with those on saprotrophic fungi. Fungal species were taken from cultures (Table 2.2.1.), which were stored in the laboratory at 15°C. Ten weeks before the start of the experiment they were inoculated on Pachlewska agar, containing per one litre distilled water 20 g glucose, 5 g maltose, 0.5 g $MgSO_4 \cdot 7H_2O$, 1 g KH_2PO_4, 0.5 g NH_4 tartrate, 50 µg thiamine HCl, 0.5 ml Fe citrate (1%), 0.5 ml ZnSO4 (0.2%) and 15 g agar. Species names of the fungi are subsequently abbreviated as genera names.

Fungi were offered on small agar discs (8 mm Ø) which were cut out of the growing front of the fungal colonies and placed in a circle of 5 cm in diameter in plastic vessels (7 cm Ø). The bottom of the vessels consisted of a layer of plaster of Paris. Five individuals of the respective oribatid mite species were placed in the centre of the vessels. After three weeks faecal pellets deposited in close vicinity of the fungal agar discs were counted and taken as a measure of the amount of food consumed, i.e. feeding preferences. There were five replicates per treatment. During the course of the experiment none of the fungal isolates became contaminated with other fungi.

Statistical analysis

The feeding preferences of oribatid mite species were analysed by single factor analysis of variance (ANOVA) with the factor ‘fungi’ (10 fungal species). For comparison of means

Tukey's honestly significant difference (HSD) was calculated (Sokal and Rohlf 1995). The food choice (number of faecal pellets) of the respective oribatid mites was analysed by one-way multivariate analysis of variance (MANOVA, Pillai's Trace; Scheiner and Gurevitch, 2001) with the factor 'fungi' with 10 levels (10 fungal species). Subsequently, protected ANOVAs (Scheiner and Gurevitch 2001) were performed to locate which of the oribatid mite species contributed to significant MANOVA results. The analyses were implemented in SAS 8e (SAS Institute Inc., Cary, USA). Data were log-transformed prior to the analysis to increase homogeneity of variance.

Table 2.2.1. Taxonomic affiliation, trophic mode and source of the ten fungal species used in this study

Fungi	trophic mode	source
Zygomycota		
Mortierella ramanniana (Møller) Linnem.	saprotroph	leaf litter of the Kranichsteiner Wald (Hesse, Germany)
Ascomycota		
Alternaria alternata (Fr.) Keissl.	saprotroph	leaf litter of the Kranichsteiner Wald (Hesse, Germany)
Cenococcum geophilum Fr.	ectomycorrhiza	fungal culture of the University of Leipzig (Germany)
Hymenoscyphus ericae (Read) Korf & Kernan	ericoid mycorrhiza	fungal culture of the Centre for Ecology & Hydrology Merlewood (UK)
Basidiomycota		
Agrocybe gibberosa (Fr.) Fayod	saprotroph	fungal culture of the Centre for Ecology & Hydrology Merlewood (UK)
Amanita muscaria (L. ex Fr.) Hooker	ectomycorrhiza	fungal culture of the University of Leipzig (Germany)
Boletus badius (Fr.) Fr.: Fr.	ectomycorrhiza	fungal culture of the Centre for Ecology & Hydrology Merlewood (UK)
Laccaria laccata (Scop.: Fr.) Cooke	ectomycorrhiza	fungal culture of the University of Leipzig (Germany)
Paxillus involutus (Batsch ex Fr.) Fr.	ectomycorrhiza	fungal culture of the University of Leipzig (Germany)
Piloderma croceum Erikss. & Hjorts	ectomycorrhiza	fungal culture of the University of Leipzig (Germany)

2.2.4. Results

Feeding of the oribatid mites significantly differed between fungal species (ANOVA, $F_{9,40} = 5.55$; $P < 0.0001$). Overall, the ericoid mycorrhizal fungus *Hymenoscyphus*, the ectomycorrhizal fungus *Boletus* and the saprotrophic fungus *Alternaria* were most preferred (Fig. 2.2.1.a). The ectomycorrhizal fungi *Laccaria, Cenococcum, Piloderma* and the saprotrophic fungus *Mortierella* were of intermediate quality whereas *Agrocybe*, *Amanita* and *Paxillus* were less preferred.

Feeding preferences of oribatid mites significantly differed between species (MANOVA, $F_{27,120} = 3.61$, $P < 0.0001$). *Oribatula tibialis* showed the strongest feeding preferences ($F_{9,40} = 8.74$, $P < 0.0001$). This species mainly fed on *Hymenoscyphus* and *Alternaria*, little on *Boletus* and *Mortierella* and rejected the other six fungi (Fig. 2.2.1.b). *Nothrus silvestris* also preferred *Hymenoscyphus*, but rejected *Agrocybe*, *Amanita* and *Boletus* ($F_{9,40} = 5.74$, $P < 0.0001$; Fig. 2.2.1.c). *Carabodes femoralis* preferred *Hymenoscyphus* and *Boletus* and also moderately fed on most of the other fungi, but only little on *Amanita* and *Paxillus* (Fig. 2.2.1.d). This species had the broadest feeding range ($F_{9,40} = 3.64$, $P = 0.0021$).

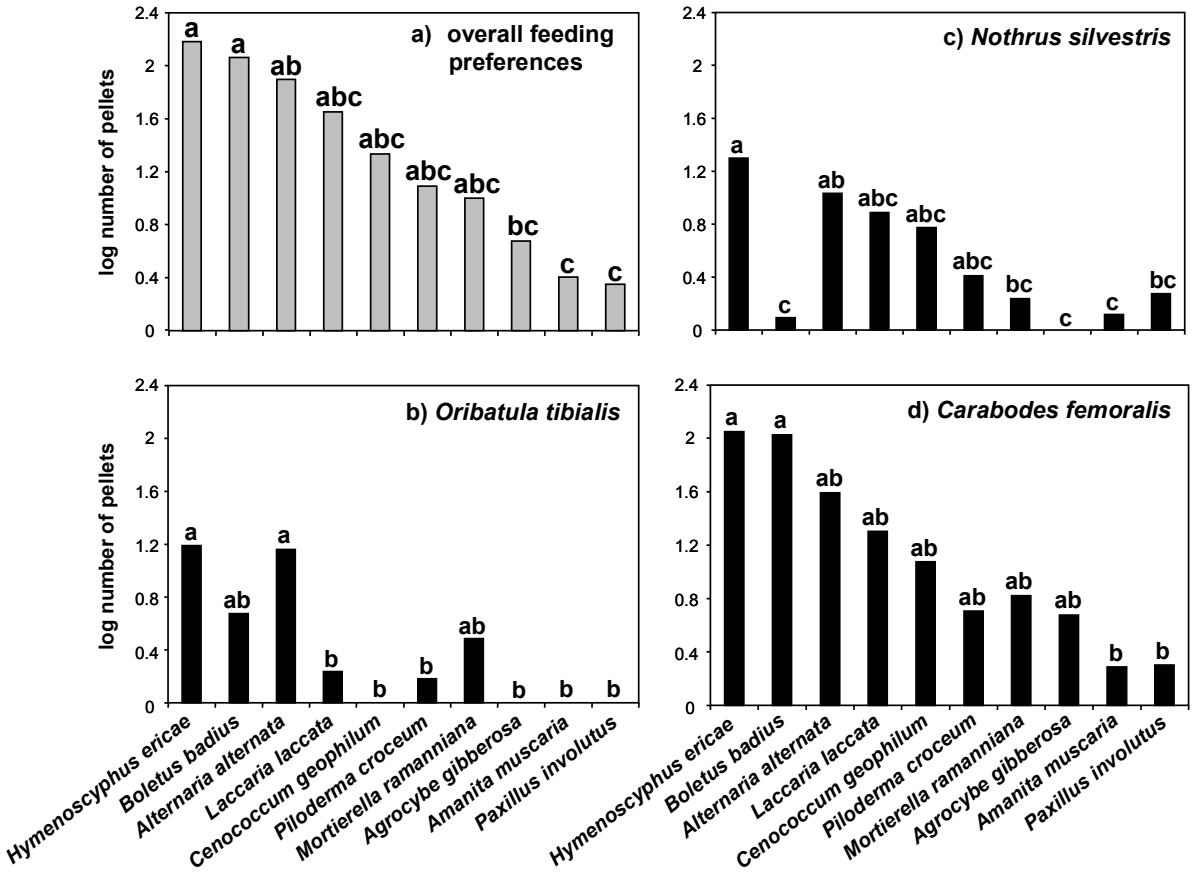

Fig. 2.2.1. Feeding preferences (number of faecal pellets) of all oribatid mites species (**a**), of *Oribatula tibialis* (**b**), *Nothrus silvestris* (**c**) and *Carabodes femoralis* (**d**) among six ectomycorrhizal fungi (*Amanita muscaria*, *Boletus badius*, *Cenococcum geophilum*, *Laccaria laccata*, *Paxillus involutus*, *Piloderma croceum*), one ericoid mycorrhizal fungus (*Hymenoscyphus ericae*) and three saprotrophic fungi *(Agrocybe gibberosa*, *Alternaria alternata*, *Mortierella ramanniana*). Fungi were offered simultaneously. Log-transformed data; bars with different letters are significantly different.

2.2.5. Discussion

Differentiation of trophic niches has been suggested to partially explain the coexistence of the high number of soil animal species (Anderson 1975a). However, studies on niche differentiation in oribatid mites yielded contradictory results. Some studies concluded that oribatid mites have a wide feeding range (Schuster 1956, Behan-Pelletier and Hill 1983, Scheu and Setälä 2002) whereas others found that oribatid mites generally prefer species of dark pigmented fungi ('Dematiacea') (Mitchell and Parkinson 1976, Maraun et al. 1998, 2003a). Furthermore, it has been shown that the feeding preferences of oribatid mite species are different among species of 'Dematiacea' (Schneider and Maraun 2005). In

addition, stable isotope analyses (^{15}N) of oribatid mite species of four forests indicated that different oribatid mite species occupy different trophic niches (Schneider et al. 2004). In the present study, I investigated ectomycorrhizal fungi as potential food resources for oribatid mites and compared the feeding on these fungi with that on saprotrophic fungi.

Feeding preferences significantly differed between the three oribatid mite species, but overall, all species preferred *Hymenoscyphus*, *Boletus* and *Alternaria*. *Alternaria* ('Dematiacea') is known to be preferred by most oribatid mite species (Hartenstein 1962, Luxton 1966, Schneider and Maraun 2005). Additionally, Ruess et al. (2000) documented that cultures of the fungal feeding nematode *Aphelenchoides* sp. could easily be established on mycorrhizal fungi, such as *Hymenoscyphus*. Studies on the interaction between nematodes and mycorrhizal fungi support these results (Giannakis and Sanders 1989, Ruess and Dighton 1996). Only one study investigated the feeding of mycophagous Collembola on ectomycorrhizal fungi (Hiol Hiol et al. 1994) and showed that *Proisotoma minuta* preferentially feeds on ectomycorrhizal fungi, such as *Laccaria laccata* and *Suillus luteus* (L.) Gray. *Laccaria laccata* was of intermediate quality in our study. Presumably, microarthropods prefer high-quality fungi (*Hymenoscyphus* and *Alternaria*) as food. High food quality commonly refers to high nutrient concentrations in food material. Beside nutritional aspects, the morphology and physiology of fungal species could also be critical for the feeding preferences of microarthropods. Fungi, such as *Mortierella*, are known to be chitinolytic (Dix and Webster 1995) and oribatid mites are captured in the long hyphae of these fungi. Oribatid mites therefore likely avoid fast growing fungal species with long hyphae and also toxic species even if the nutrient value of that fungus is high. Fungal species with short hyphae, e.g. *Alternaria* and *Hymenoscyphus*, are likely ingested. Mills and Sinha (1971) concluded that the morphology of mycelia is an important factor for the collembolan *Hypogastrura tullbergi* (Collembola), which had higher reproduction rates on

fungi with low spore count and a mycelia mat that allowed free movement, than on fungi with a thick layer of powdery spores and a dense mycelia mat.

In addition to the ectomycorrhizal fungi I also offered three saprotrophic fungi as potential food resource for oribatid mites to estimate the quality of the ectomycorrhizal fungi. These three saprotrophic fungi were of different food quality as indicated from former food choice experiments (Maraun et al. 1998a, Ruess et al. 2000, Schneider and Maraun 2005). Some mycorrhizal fungi were even more intensively consumed than the high-quality saprotrophic fungus *Alternaria* suggesting that the feeding of oribatid mites on the mycorrhizal fungi is likely important in the field.

In contrast to the results of the food choice experiment of Schneider and Maraun (2005), *Oribatula tibialis* showed strong feeding preferences in this study. *Nothrus silvestris*, also ascribed to unspecialized species (Maraun et al. 1998a, Schneider and Maraun 2005), clearly selected certain ectomycorrhizal fungal species. Additionally, the selective feeding of *Carabodes* (Schneider and Maraun 2005) was not supported by results of this study. I speculate, that oribatid mites that mainly feed on fungi form two feeding guilds. Some oribatid mite species prefer mycorrhizal fungi, whereas others prefer saprotrophic fungi. Moreover, oribatid mites of both feeding guilds selectively feed on different fungi within the respective group (saprotrophic or mycorrhiza), but in case of shortage of the preferred food they are also able to feed on other (low-quality) fungi. The lack of a narrow specialisation of oribatid mites may be the consequence of fluctuating availability of the preferred (high-quality) food in the field. Nevertheless, results of this experiment suggest that trophic niche differentiation at least in part contributes to the understanding of the high number of oribatid mites in soil since feeding on mycorrhizal fungi increases the niche space by at least one dimension.

Feeding on ectomycorrhizal fungi may affect fungal biomass and changes in fungal community structure, which may have far-reaching consequences for decomposition rates,

nutrient cycling and plant growth as shown for collembolan grazing on VA mycorrhizal fungi (Warnock et al. 1982, Finlay 1985, Harris and Boerner 1990, Gange and Brown 1992). The effects of microarthropod grazing on ectomycorrhizal fungi have hardly been studied (but see Hiol Hiol et al. 1994). There is a need for studies investigating the influence of oribatid mites on ectomycorrhizal fungi and plant performance.

2.3. Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/^{14}N$)

2.3.1. Abstract

The large number of animals that co-exist in soil without any clear niche differentiation has puzzled biologists for a long time. I investigated stable isotope ratios ($^{15}N/^{14}N$) in a diverse group of soil microarthropods, oribatid mites, to evaluate trophic niche differentiation. The natural variation of the stable isotopes $^{15}N/^{14}N$ was measured in 36 species/taxa from four beech and beech-oak forests. Signatures of $\delta^{15}N$ formed a gradient spanning over 12 δ units suggesting that (a) different species occupy different trophic niches and (b) oribatid mites span three to four trophic levels. This study for the first time documented strong trophic niche differentiation in decomposer microarthropods. The results suggest that trophic niche differentiation within taxonomic groups significantly contributes to the high diversity of soil animal taxa.

2.3.2. Introduction

It remains a riddle to soil biologists how the large number of soil decomposer animal species coexists without extensive niche differentiation (Anderson 1975a). One of the most important decomposer groups are soil microarthropods such as oribatid mites that are species rich and reach high densities (Maraun and Scheu 2000). They contribute significantly to decomposition processes and nutrient turnover (Visser 1985). Oribatid mites consist of about 10,000 named species and the total number of their species is estimated to be up to 100,000 (Schatz 2002). The α- (or local-) diversity of oribatid mites is high, e.g. in litter and soil of a southern Appalachian hardwood forest 170 species coexist (Hansen 2000).

Analysis of the natural variation in stable isotope ratios in animal tissue has been shown to be a powerful tool in evaluating the trophic structure of animal communities (Minagawa and Wada 1984, Wada et al. 1991, Ponsard and Arditi 2000, Scheu and Falca 2000). In contrast to gut content analyses and food choice experiments, stable isotope ratios reflect the long-term trophic relationships of animals. Animal tissues are more enriched in ^{15}N than their food source (DeNiro and Epstein 1981) by a constant value of 3.4 δ units per trophic level (Post 2002).

Oribatid mites have been separated into three different trophic groups by Schuster (1956): (1) macrophytophagous species that feed on wood, roots and litter material, (2) microphytophagous species that feed on fungi, pollen, algae, mosses and lichens and (3) non-specialized species that combine the feeding habits of macro- and microphytophagous species. Luxton (1972) further distinguished: zoophagous, necrophagous and coprophagous species. Others grouped oribatid mites according to their cheliceral dimensions (Kaneko, 1988) or their enzymatic capabilities (Siepel and de Ruiter-Dijkman 1993). There are, however, difficulties in assigning oribatid mites to functional groups: laboratory studies, which form the basis of some classifications, may not reflect feeding in the field, cheliceral sizes may not be correlated with the actual food substrate used and studies on gut enzymes may be misleading because enzyme activities may depend on recently ingested food and on functionally insignificant enzymes from ingested microorganisms. Furthermore, it is difficult to separate species that feed on plant litter material from those species that feed on fungi inside the litter (but consume the litter to gain access to the fungal material). In addition, some immature oribatid mites (e.g. Ptyctima, *Cepheus* sp., *Liacarus* sp., *Adoristes* sp., *Carabodes* sp.) are mostly or strictly endophagous in solid higher plant remains, whereas their adults range freely in litter and may selectively feed on quite different food substrates (Lions and Gourbière 1988, Migge et al. 1998).

I have analysed the $^{15}N/^{14}N$ ratios of soil-living oribatid mites of four forests to evaluate whether oribatid mite species occupy distinct niches with respect to food resources, irrespective of the habitat (forest type) they occupy. I expected trophic differentiation in oribatid mite species to be low since they are thought to be food generalists and niche differentiation between species is low (Maraun et al. 1998, Scheu and Setälä 2002).

2.3.3. Materials and Methods

Study sites

In October 2002 oribatid mites were extracted from litter samples of four forests: Kranichsteiner Wald (KW), Göttinger Wald (GW), Solling (SO) and Wohldorfer Wald (WW). In addition, oribatid mites were extracted from the bark of beech trees (SB) in the Solling. The Kranichsteiner Wald is an oak-beech forest, located c. 8 km northeast of Darmstadt, southern Germany, at 150-175 m a.s.l. Parent rock is Rotliegendes covered with sand. The soil types are dystric gleysols and orthic luvisols (FAO-UNESCO classification); the humus form is a typical moder. The pH of the soil varies between 3.6 and 4.3. The tree layer is dominated by oak (*Quercus robur*), c. 190 y old, with interspersed beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*). The herb layer is dominated by *Luzula luzuloides*, *Milium effusum*, *Anemone nemorosa*, *Oxalis acetosella*, *Deschampsia cespitosa*, *Stellaria holostea*, *Melampyrum pratense* and *Polytrichum formosum*. The Göttinger Wald is a beech forest (*F. sylvatica*), c. 130 yr old, located on a limestone plateau east of Göttingen, North Germany, at 420 m a.s.l. Maple (*Acer platanoides* and *A. pseudoplatanus*) and ash trees (*Fraxinus excelsior*) are interspersed. The herb layer is rich in species but dominated by *Allium ursinum*, *Mercurialis perennis* and *Anemone nemorosa* (Dierschke and Song 1982). The soil is of the orthic rendzina type with typical mull humus. The pH of the soil varies between 4.4 and 7.0 and is on average 5.3.

The Solling is a mature beech (*F. sylvatica*) stand of c. 135 y, located c. 50 km northwest of Göttingen (Lower Saxony, Germany). The Solling is a mountain range at 500 m a.s.l. Parent rock is sandstone covered with a loess layer of about 1 m. The soil type is a dystric cambisol with a moder humus. Litter and soil pH in the Solling are low (between 3.3 and 4.4). The understory is formed mainly by small patches of *Luzula luzuloides*. The Wohldorfer Wald is an oak-beech forest, c. 200 y old, located c. 20 km northeast of Hamburg, North Germany, at 20-32 m a.s.l. Parent rock is boulder clay partially covered with sand. The soil is of the dystric gleysol and orthic luvisol types with the humus form moder. Soil pH varies between 3.5 and 4.8. The tree layer is dominated by beech (*F. sylvatica*) but other species are interspersed, including *Quercus robur*, *Alnus glutinosa*, *Betula pendula*, *Fraxinus excelsior* and *Acer* spp.

Sampling and ^{15}N analysis

In each forest the L/F layer material from five sites, 5 m apart, was collected and transferred to the laboratory, where oribatid mites were extracted using a high gradient extractor (Macfadyen 1961, Kempson et al. 1963). Additionally, in the Solling, oribatid mites were extracted from the bark of trees. Oribatid mites were collected in water, separated under a dissecting microscope and determined to species or higher taxonomic level, and transferred to 70% ethanol. Storage in ethanol does not significantly affect the $^{15}N/^{14}N$ signature of soil arthropods (Fabian 1998). For measurement of their $^{15}N/^{14}N$ ratios oribatid mites were transferred to tin capsules and dried at 60°C. After 24 h the samples were weighed and stored in a desiccator until analysed. Replicates of species or taxa were analysed in each of the forests if possible. Each sample consisted of pooled individuals (3 to 255 individuals) to obtain sufficient material for ^{15}N analysis.

In addition to the animals, material from the L/F layer of each forest (five replicates) and from tree bark (three replicates) in the Solling, which were separated into four thin layers (ranging from a lichen-rich outer material to deeper bast layers) were analysed. Samples were dried (60°C), milled, weighed in tin capsules and stored in a desiccator until analysed.

The $^{15}N/^{14}N$ ratios of animals, soil and bark were determined by a coupled system of an elemental analyser (NA 1500, Carlo Erba, Milan) and a mass spectrometer (MAT 251, Finnigan). The system is computer controlled, allowing on-line measurement of ^{15}N. Stable isotope abundance is expressed using the δ notation with $\delta^{15}N$ (‰) = $(R_{sample}-R_{standard})/R_{standard}$x1000. R_{sample} and $R_{standard}$ represent the $^{15}N/^{14}N$ ratios of the sample and standard, respectively. For ^{15}N atmospheric N_2 served as the primary standard and acetanilide (C_8H_9NO, Merck, Darmstadt) for internal calibration. The mean standard deviation of samples of 10-200 µg N, the range of the samples measured, is 0.2‰ (Reineking et al. 1993).

To allow comparison of $\delta^{15}N$ values for oribatid mite species from different forests, the $\delta^{15}N$ signatures of the animals of the Göttinger Wald, the Kranichsteiner Wald and the Wohldorfer Wald were corrected by the difference between $\delta^{15}N$ values of the L/F layer of these forests to that of the Solling (–3.56).

2.3.4. Results

Litter and bark

The $\delta^{15}N$ signatures of the L/F material from the Solling and the Göttinger Wald were almost identical (-3.56, SD = 0.13 and -3.68, SD = 0.31, respectively). In contrast, $\delta^{15}N$ signatures of the L/F layer of the Kranichsteiner Wald (-4.22, SD = 1.02) and the Wohldorfer Wald (-6.06, SD = 0.08) were significantly lower. The $\delta^{15}N$ values of the bark

of the beech trees were -3.65, -2.58, -0.05, 0.59 for the outer bark layer and the three inner layers, respectively.

Variation in oribatid mite $\delta^{15}N$ signatures

The range of $\delta^{15}N$ signatures among oribatid mite species differed markedly in each of the four forests (Fig. 2.3.1.). Overall, $^{15}N/^{14}N$ ratios formed a continuous gradient spanning over 12 δ units, but the gradient varied between the forests. In the Kranichsteiner Wald it ranged between -4.22 (*Achipteria coleoptrata*) and -0.76 (*Nothrus silvestris*), in the Göttinger Wald between -3.74 (*Platynothrus peltifer*) and 4.39 (*Amerus troisii*), at the Solling between -3.27 (*Carabodes marginatus*) and 2.48 (*Hypochthonius rufulus*) and in the Wohldorfer Wald between -7.74 (*Carabodes labyrinthicus*) and 1.47 (*Pilogalumna* spp.) (calibrated data).

$^{15}N/^{14}N$ ratios of individual oribatid mite species

With few exceptions (*Rhysotritia duplicata*, Phthiracaridae, *Galumna* spp. and *Nothrus silvestris*) the $^{15}N/^{14}N$ ratio of a given species differed little among forests (Fig. 2.3.1.). Less enriched species included *Carabodes labyrinthicus*, *Achipteria coleoptrata*, *Carabodes marginatus*, *Platynothrus peltifer*, *Nothrus palustris*; more enriched species included *Nothrus silvestris*, *Pilogalumna* spp., Oppiidae & Suctobelbidae, *Hypochthonius rufulus* and *Amerus troisii*.

Even in species of the same genus $^{15}N/^{14}N$ ratios differed significantly. Species of *Carabodes* formed a gradient from *Carabodes labyrinthicus* to *C. femoralis*, with *C. marginatus* being intermediate (Fig. 2.3.1.). Similarly, $^{15}N/^{14}N$ ratios of the two species of *Nothrus* (*N. silvestris* and *N. palustris*) and of *Nanhermannia* (*N. nana* and *N. coronata*) differed strongly. In contrast, $^{15}N/^{14}N$ ratio varied little among the three species of

Chamobates (*Ch. cuspidatus*, *Ch. borealis* and *Ch. voigtsi*). In *Nothrus palustris* of the Göttinger Wald $^{15}N/^{14}N$ ratios differed little between juvenile (-2.80) and adult (-3.56, SD= 0.13) stages.

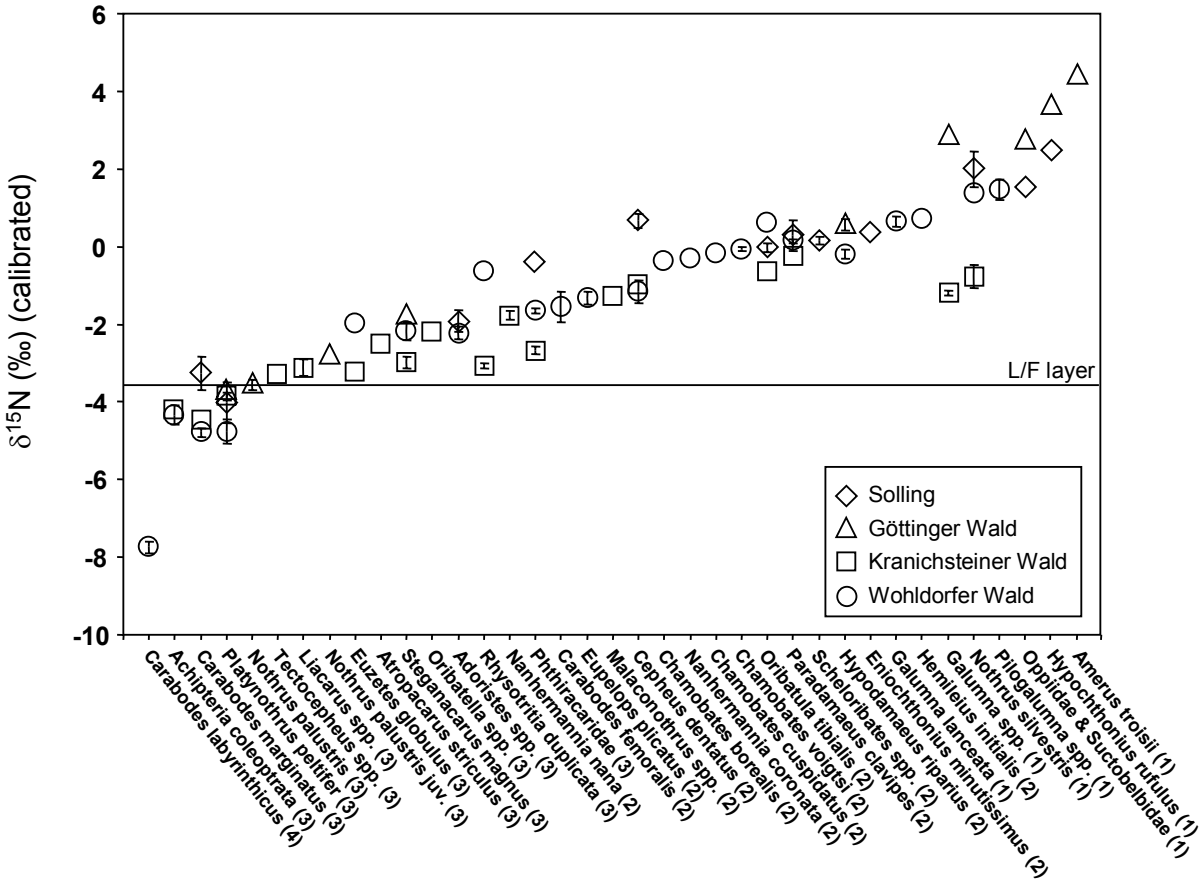

Fig. 2.3.1. Variation of $\delta^{15}N$ values of oribatid mites from four different beech forests. Data calibrated to the L/F litter material of the Solling (L/F layer). Single measurements (without SD) and means of 2-5 replicates with SD. If no line is shown only a single analysis was made. Species were ordered according to increasing $\delta^{15}N$ value. Numbers in brackets indicate feeding guilds (see Fig. 2).

The $^{15}N/^{14}N$ ratios of bark-dwelling mites from the Solling were similar to that of litter-dwelling mites at this site (Table 2.3.1.). *Zygoribatula exilis* ($\delta^{15}N = 0.82$, SD = 0.02) was the only species that was found exclusively on bark.

Table 2.3.1. $\delta^{15}N$ values and N contents of the bark-dwelling oribatid mites of the Solling. Δ litter: differences in $\delta^{15}N$ values of the same species from the L/F layer.

species	$\delta^{15}N$ value [‰] ± SD	Δ litter (^{15}N)*
Paradamaeus clavipes	3.02 ± 0.58	2.75
Cepheus dentatus	1.35	0.69
Adoristes sp.	-0.95	1.08
Tectocepheus velatus	-2.57	-
Carabodes marginatus	-3.10 ± 0.12	0.17

* Δ litter: differences in $\delta^{15}N$ values of the same species from the L/F layer

2.3.5. Discussion

Resource partitioning is one of the main drivers of species diversity and composition in animal communities (Schoener 1974). However, in contrast to above-ground systems the role of trophic niche differentiation to account for the diversity of decomposer communities remains obscure. Therefore, belowground animal species diversity could not be explained by Hutchinsonian niche differentiation.

Differentiation of trophic niches has been suggested to explain partially the coexistence of the high number of soil living animal species (Anderson 1975a, b). However, laboratory food choice experiments of decomposer invertebrates indicate wide overlap in food resources among species with, e.g. most fungal feeding species prefering similar fungal taxa (Maraun et al. 2003a).

Our results document for the first time that oribatid mite species occupy very different trophic niches. The $\delta^{15}N$ values of oribatid mites spanned over a range of 12 δ units. Assuming an enrichment of 3.4 ‰ per trophic level (DeNiro and Epstein 1981, Minagawa and Wada 1984, Post 2002), this is equivalent to three to four trophic levels. However, ascribing decomposer invertebrates to trophic levels by using $^{15}N/^{14}N$ ratios is not

straightforward. $\delta^{15}N$ values of decomposer animals may reflect feeding guilds rather than trophic groups (Scheu 2002). For interpretation of the natural variation of ^{15}N ratios in microbi-detritivorous soil animals it is a precondition to know to what extent bacteria, fungi and algae fractionate stable isotopes. The fractionation of stable isotopes in fungi differs between species (Scheu and Folger 2004) but it may generally be low (Kohzu et al. 1999). Therefore, I emphasize that data on variation in stable isotope ratios in fungal feeding animals have to be interpreted with caution. For example, if a fungus growing on a dead microarthropod is consumed by another soil animal the resulting ^{15}N value of the fungal feeding animal might be very high. Consequently, this animal is (wrongly) ascribed to the predator feeding guild. However, such an experiment has never been carried out.

Carnivorous and omnivorous oribatid mites

Amerus troisi had the highest ^{15}N signature, 8 δ units higher than the litter, suggesting that this species lives predominantly on an animal diet, possibly of nematodes. Similarly, high $\delta^{15}N$ signatures of *Hypochthonius rufulus* indicate that this species lives on animal prey. Indeed, *H. rufulus* has been observed to feed on dead collembolans and 'worms' (Riha 1951), but fungal feeding is more commonly reported (Schuster 1956, Hartenstein 1962, Luxton 1972, Maraun et al. 1998a). Galumnidae (especially *Pergalumna* spp.) also had high $\delta^{15}N$ signatures and are known to feed on a variety of resources including living nematodes (Rockett and Woodring 1966, Muraoka and Ishibashi 1976, Rockett 1980) and collembolans (Wunderle 1992). The $\delta^{15}N$ signatures of the above mentioned oribatid mite taxa were similar to those of predatory Mesostigmata as reported by Scheu and Falca (2000). Therefore, I assigned these species to the carnivores/scavengers/omnivores feeding guild (Fig. 2.3.2.).

Based on a shift of 3.4 δ units per trophic level I distinguished three other guilds: (1) secondary decomposers; predominantly feeding on fungi and partly on litter (2) primary decomposers; feeding on litter little colonized by fungi and bacteria (3) phycophages/fungivores; feeding mainly on lichens and algae (Fig. 2.3.2.).

	oribatid mite taxa	feeding guild	food materials
1	*Amerus troisii* *Hypochthonius rufulus* Oppiidae/Suctobelbidae *Nothrus silvestris* Galumnidae	carnivores/ scavengers/ omnivores	living and dead animals (nematodes, collembolans) and fungi
2	*Eniochthonius minutissimus* Damaeidae Oribatulidae/Scheloribatidae Chamobatidae *Nanhermannia coronata* *Cepheus dentatus* *Malaconothrus* spp. *Eupelops plicatus* *Carabodes femoralis* *Nanhermannia nana*	secondary decomposers	predominantly fungi, in part litter
3	Ptyctima *Adoristes* spp. *Oribatella* spp. *Euzetes globulus* *Liacarus* spp. *Tectocepheus* spp. *Nothrus palustris* *Platynothrus peltifer* *Carabodes marginatus* *Achipteria coleoptrata*	primary decomposers	predominantly litter
4	*Carabodes labyrinthicus*	phycophages/ fungivores	lichens and algae

Fig. 2.3.2. Schematic representation of the trophic structure (feeding guilds 1-4) and possible food resources of oribatid mites from four different beech forests, as indicated by their $^{15}N/^{14}N$ ratios. Species that belonged to similar taxa and also had similar ^{15}N signatures were grouped at higher taxonomic levels: Galumnidae (incl. *Pilogalumna* spp., *Galumna* spp., *Galumna lanceata*), Damaeidae (*Paradamaeus clavipes*, *Hypodamaeus riparius*), Oribatulidae/Scheloribatidae (*Hemileius initialis*, *Scheloribates* spp., *Oribatula tibialis*), Chamobatidae (*Chamobates voigtsi*, *Ch. cuspidatus*, *Ch. borealis*), Ptyctima (*Steganacarus magnus*, *Phthiracarus* spp., *Atropacarus striculus*, *Rhysotritia duplicata*).

Secondary decomposers

Secondary decomposers consisted of species with $\delta^{15}N$ values spanning from 0.35 to -1.78. The species with the highest ^{15}N signatures of this group are *Eniochthonius minutissimus*, Damaeidae, Oribatulidae/Scheloribatidae, Chamobatidae and *Nanhermannia coronata* which have been reported to predominantly feed on litter material and microorganisms (Schuster 1956, Luxton 1972, Pande and Berthet 1973, Muraoka and Ishibashi 1976, Kaneko 1988, Siepel and de Ruiter-Dijkman 1993). Presumably, these taxa feed mainly on fungi but also partly on decomposing litter material. I assume that the other taxa of the fungal/litter feeder group (*Cepheus dentatus*, *Malaconothrus* sp., *Eupelops plicatus*, *Carabodes femoralis* and *Nanhermannia nana*) predominantly feed on litter material but also ingest fungi that colonize this litter (Fig. 2.3.2.). Previously, they have been assigned to very different feeding guilds (Riha 1951, Schuster 1956, Luxton 1972, Kaneko 1988, Siepel and de Ruiter-Dijkman 1993).

Primary decomposers

Oribatid mite species with $\delta^{15}N$ signatures similar to the signature of the L/F layer (-1.99 to -4.28) such as Ptyctima, *Adoristes* sp., *Oribatella* sp., *Euzetes* sp., *Liacarus* sp. presumably primarily live on decomposing plant material (primary decomposers; Fig. 2.3.2.). Ptyctima and other oribatid mite species often colonize litter material for feeding and egg deposition (Jacot 1939, Lions and Gourbière 1988, Migge et al. 1998, Hansen 1999). The juveniles of these species are endophagous, living inside litter and needles. Other species of this group are known to feed on decaying litter and algae (Riha 1951, Schuster 1956, Luxton 1972, Kaneko 1988, Siepel and de Ruiter-Dijkman 1993). *Tectocepheus* is known to feed on a variety of resources ranging from lichens to fungi (Hartenstein 1962, Siepel and de Ruiter-Dijkman 1993).

Phycophagous and fungivorous oribatid mites

The $\delta^{15}N$ signatures of *Carabodes labyrinthicus* were much lower than those of all other oribatid mites. *C. labyrinthicus* predominantly colonises the bark of trees (Wunderle 1992) but occasionally is found on the forest floor. Immatures of *Carabodes* species burrow in wood, fungal sporophores or lichens (Hansen 1999). The food of adult *C. labyrinthicus* include lichens on the bark of trees and algae (Smrz and Kocourkova 1999, Materna 2000). Litter at the forest floor is colonised by algae during most of the year (Wohler et al. 1998), and *C. labyrinthicus* is also likely to feed on lichens and algae in the litter. Therefore, the species was assigned to phycophages/fungivores (Fig. 2.3.2.). Generally, $\delta^{15}N$ signatures from bark living oribatid mite species differed little from those of litter species. Obviously, a given oribatid mite species feeds on similar resources regardless of the habitat in which it lives.

A striking feature of our results is that species with very similar morphology either had very similar or very different $\delta^{15}N$ signatures. The $\delta^{15}N$ signatures of *N. silvestris* were high (2.01) whereas those of *N. palustris* were low (-3.56) suggesting that the two species live on very different diets. The $\delta^{15}N$ signatures of species of *Carabodes* also differed strongly (*C. labyrinthicus* -7.74, *C. marginatus* -3.29 and *C. femoralis* -1.55) suggesting different diets for each of the species. Differential feeding of morphologically similar species supports the conclusion of Scheu and Falca (2000) that higher taxonomic units are of very limited use for depicting trophic groups.

Previously, it has been assumed that oribatid mites are generalist feeders with little trophic niche differentiation (Maraun et al. 1998a, Scheu and Setälä 2002). In striking contrast to these assumptions our results indicate that oribatid mite species, despite being generalist feeders, occupy distinct trophic niches. The wide range of $\delta^{15}N$ signatures of oribatid mites and their constant trophic position in different forest habitats suggests that

partitioning of food resources between species significantly contributes to the high diversity of oribatid mite species. Trophic niche differentiation despite generalist feeding may also contribute to the diversity of other soil invertebrate taxa, such as Collembola, Nematoda and Protozoa.

2.4. Oribatid mite and collembolan diversity, density and community structure in a moder beech forest (*Fagus sylvatica*): effects of mechanical perturbations

2.4.1. Abstract

The effects of mechanical perturbations on two soil microarthropod communities (oribatid mites and collembolans) were investigated in a moder beech forest on sandstone. I disturbed the soil matrix by sieving and mixing the litter and soil of the moder profile. The top litter layer (L material) and the deep mineral soil (Bv) remained intact. Three amounts of disturbance were established: a single perturbation, perturbations once every two month (60 d) and once every two weeks (14 d). Densities of most groups of oribatid mites and all groups of collembolans declined in the disturbance treatments. In most cases, densities were lowest in the strong perturbation treatment (14 d). Desmonomata were the only group of oribatid mites that benefited from intermediate amounts of disturbance but not from the strongest disturbance. Also, disturbances reduced diversity of oribatid mites. According to their sensitivity to disturbances oribatid mites ranked Poronota = Enarthronota = Suctobelbidae (the most sensitive) > Oppiidae > *Tectocepheus* > Desmonomata. The ranking of collembolans was *Folsomia* (the most sensitive) > Hypogastruridae/Neanuridae > Onychiuridae = Isotomidae > Entomobryidae. Generally, tolerance of disturbance was wider for oribatid mites than for collembolans. The results indicate that disturbances such as mixing of litter and soil and comminution of litter material strongly affect the density and diversity of soil microarthropods. However, they also indicate that the soil microarthropod community is resistant to weaker disturbances. In the field, mechanical disturbances are often caused by burrowing of earthworms. Our results suggest that the high density of microarthropods in moder soils may be due to the low intensities of mechanical disturbances by earthworms.

2.4.2. Introduction

Environmental factors that prevent organisms from exponential growth by causing density-independent mortality can be regarded as disturbances. Biotic and abiotic factors may function as disturbances (Pickett and White 1985). They can be predictable or unpredictable, e.g. temperature fluctuations in the temperate regions are predictable for seasonal changes but are unpredictable for long-term fluctuations caused by for example El Niño events or volcanic eruptions. Biotic factors may also be predictable (constant predator pressure) but also unpredictable (introduction of an invader into a food web). Some organisms may be adapted to predictable but not to unpredictable disturbances. Especially slow reproducing species are usually adversely affected by unpredictable disturbances. Unpredictable disturbances function as pulse perturbations striking the system at irregular intervals and then leaving it to recover. The system may return to the former state at a certain speed, stay in the shifted state or resist the disturbance (Bender et al. 1984). A system that will infrequently be affected by disturbances likely exists close to equilibrium conditions except after a disturbance. In contrast, repeated disturbances function as press perturbations keeping the system away from equilibrium conditions (Bender et al. 1984).

Disturbance regimes affect species diversity. Connell (1978) postulated that intermediate degrees of biotic or abiotic disturbances reduce the intensity of competition between species and hence the competitive exclusion of species (intermediate disturbance hypothesis; Grime 1973, Horn 1975, Connell 1978). The intermediate disturbance hypothesis was further elaborated by Huston (1979, 1994); he included the interaction between the intensity of the disturbances and the growth rate of the population at a specific site. High levels of diversity are maintained at sites where the intensity of the disturbance and the growth rate of the population are similar, i.e. few disturbances maintain high diversity in communities where the average reproduction rate is low and high intensities of

disturbances maintain high diversity in communities where the average reproduction rate is high. Highest diversity occurs when there is a balance between disturbance and competitive exclusion. By occurring at different times at different sites, disturbances also create habitat patches that differ from each other. In this mosaic of patches succession of species will be at different stages and while some species may be absent from one patch the same species may flourish in another patch. Migration occurs between the patches but, due to disturbances, competitive exclusion is avoided. This 'patch-dynamic' view (cf. Huston 1979) explains the high diversity of animal and plant communities by allowing coexistence of species even though their niches overlap widely.

Our aim was to understand the reason for the high diversity of soil microarthropods in temperate forest ecosystems. In contrast to the intermediate disturbance hypothesis, there is increasing evidence that even moderate amounts of disturbance reduce the diversity and density of soil microarthropods (Scheu and Schulz 1996, Maraun et al. 1999, 2001). I therefore hypothesized that increasing amounts of disturbance gradually decreases the density and diversity of oribatid mites and collembolans. Within oribatid mites and collembolans, I hypothesized that parthenogenetic taxa and fast reproducing species would profit from disturbances while sexual species and slow reproducing species would suffer most. The community structure of oribatid mites changes strongly during secondary succession from agricultural sites to fallows and forests (Scheu and Schulz 1996) and it has been speculated that these changes are driven by different intensities of disturbances (Maraun and Scheu 2000). To investigate how different amounts of disturbance influence the density, diversity and community structure of soil microarthropods I exposed the soil animal community of a beech forest on sandstone to a single perturbation and two intensities of periodic perturbation (once every two month (c. 60 d), once every two weeks (c. 14 d)).

Earthworms may cause periodic disturbance for soil microarthropods in deciduous forests. Especially in calcareous forests, high densities of endogeic and anecic earthworms can be regarded as agents of disturbance (Maraun and Scheu 2000). Earthworms feed on organic materials, mix organic layers with the mineral soil and consequently reduce the habitat size (the litter layer) and the amount of available resources (decomposing litter and soil fungi) for soil microarthropods. Other effects include the alteration of the fungal community and the damage or destruction of egg clutches of soil microarthropods (Maraun et al. 2001). Earthworm activities can detrimentally affect soil microarthropod communities, i.e. reduce their densities and change their community structure (Maraun et al. 1999, McLean and Parkinson 1998, 2000, Maraun and Scheu 2000). Oribatid mites, especially, have been shown to be very sensitive to disturbances (Norton and Palmer 1991).

The evidence that earthworms detrimentally affect soil microarthropods mainly resulted from laboratory experiments (S. Migge, pers. comm.) and from comparisons of microarthropod densities and community structure from different forest types with large and small densities of earthworms (Maraun and Scheu 2000). Only rarely has the density of earthworms been manipulated in field experiments to evaluate the response of soil microarthropods (S. Migge, pers. comm.). The disturbance regimes set up in this experiment were chosen to obtain a better understanding on the role of disturbance agents such as earthworms on microarthropod community structure in temperate forest soils.

2.4.3. Material and Methods

Study site

The study site, a mature beech (*Fagus sylvatica* L.) stand of an age of c. 135 y, is located 50 km northwest of Göttingen in the Solling forest (Lower Saxony, Germany). The Solling is a mountain range of about 400 km² at 500 m a.s.l. Parent rock is sandstone covered with

a loess layer of about 1 m. The soil type is an acidic brown-earth with the humus form moder. The average annual precipitation is 1045 mm and the average annual temperature is 6.5 °C (Ellenberg et al. 1986). Litter and soil pH in the Solling are low (3.3 and 3.2, respectively). The site was chosen for the experiment because the influence of disturbance, especially earthworm activity, is low.

Experimental design and sampling

In August 1998 20 circular experimental plots with an area of 1 m² were established. The plots were enclosed by PVC rings of 40 cm height that were dug in the soil to a depth of about 10 cm. The litter (L-layer) was removed and placed into a plastic container. Then, F-H- and Ah-layers were removed to a depth of 10-15 cm and sieved (1 cm²). The material was then placed back into the plots and the L-layer was added on top. The L-layer was not sieved to avoid drying of the soil-litter mixture. Plots without further disturbance were used for the single (S) perturbation treatment. Plots for the perturbation treatment 'once every two month' (60 d; BM) and 'once every two weeks' (14 d; BW) were manipulated in the same way repeatedly; for the BM disturbance treatment it was repeated once in October 1998 and for the BW disturbance treatment it was repeated seven times (end of August, beginning and end of September, October and November). Undisturbed plots served as controls (C). Five replicates were set up per treatment.

In December 1998, after 4 months of the experimental regime, soil microarthropods were sampled by taking soil cores of 5 cm diameter (one soil core per plot). I separated the horizons L, F-H/Ah and Bv and extracted soil microarthropods using heat extraction (Macfadyen 1961). Collembolans were determined to genus or family level by J.-A. Salamon (Entomobryidae, *Folsomia*, Hypogastruridae/Neanuridae, Isotomidae, Onychiuridae). Oribatid mites were determined to species or genus level by myself. Oribatid mites were separated into juveniles and adults; parthenogenetic and sexual species

were distinguished according to Norton et al. (1993). For the statistical analysis oribatid mite species were arranged in taxonomic groups (Enarthronota, Desmonomata, *Tectocepheus*, Oppiidae, Suctobelbidae, Poronota; see Appendix).

Statistical analysis

Abundances of oribatid mites, juvenile and parthenogenetic oribatid mites and collembolans were analysed by analysis of variance (ANOVA) using SAS 8e (SAS Institute Inc., Cary, USA). Effects of perturbation (control, single perturbation and the rates of two perturbations) and horizon (L-layer, intermediate layer, soil) were analysed. However, due to limited effects of the factor 'horizon' (reduction of density of most soil animal taxa with soil density but no interaction of 'horizon' with other factors investigated) I pooled the data on soil microarthropods for this factor. For comparison of means Tukey's honestly significant difference was calculated.

The response of taxonomic groups of oribatid mites and collembolans was analysed by one-way multivariate analysis of variance (MANOVA, Pillai's Trace; Scheiner and Gurevitch 2001) with the fixed factor 'perturbation' studied at four rates (control, single, once every two month (BM), once every two weeks (BW)). To estimate which of the taxa contributed most to the effects detected by the MANOVA, separate ANOVAs for these taxa were performed ('protected ANOVA', cf. Scheiner and Gurevitch 2001). Data were log-transformed prior to the analysis to increase homogeneity of variances.

A discriminant function analysis (DFA) was carried out with the abundance data of all species of Oribatida and Collembola together to investigate if the community structure of the microarthropods differed between disturbance regimes. Squared Mahalanobis distances between group centroids were calculated to evaluate significant differences among disturbance regimes.

Before the DFA I performed a multidimensional scaling (MDS). MDS generates a distance matrix (distances between the sites) that regroups the samples in n-dimensional space. The quality of the new configuration is indicated by the stress value. Low dimensions in the distance matrix increase the stress values but erase the background noise while high dimensions usually reduce the stress but increase the background noise (Backhaus et al. 1996). The best compromise for this trade-off for the data of this experiment was found for four dimensions. Calculations for DFA and MDS were carried out in STATISTICA 5.0 (Statsoft Inc., Tulsa, USA).

2.4.4. Results

General effects of perturbation

Single and repeated perturbations strongly reduced the abundance of oribatid mites and collambolans and the number of oribatid mite species. The influence of the perturbations was different for different taxa and species of oribatid mites and collembolans.

In the control and in the single perturbation treatment 16 oribatid mite species were present which were reduced to 14 in the BM treatment and to 7 in the BW treatment (ANOVA: $F_{3,16} = 22.2$, $P < 0.0001$). Brachychthonidae and Suctobelbidae were not determined to species level and therefore not included in this calculation.

Density of oribatid mites and collembolans

The density of oribatid mites was gradually reduced with increasing intensity of perturbations (ANOVA: $F_{3,16} = 14.9$, $P < 0.0001$). However, this reduction was not significant for the single perturbation and the bi-monthly perturbation but for the BW perturbation (Fig. 2.4.1.). Oribatid mite density generally was highest in the F/H/Ah layer (25,874 ind m^{-2}) and significantly lower in the L and Bv layer (2598 and 2982 ind m^{-2}, respectively).

The density of collembolans also declined with the intensity of perturbations but the reduction was much stronger compared to oribatid mites (ANOVA: $F_{3,16} = 19.5$, $P < 0.0001$). The single pulse perturbations reduced the density to 57 % and the two periodic perturbations to 33 % and 13 % of the control (Fig. 2.4.1.). Similar to oribatid mites, the density of collembolans generally was highest in the F/H/Ah layer (10,501 ind m^{-2}) and lowest in the L layer and the mineral soil (1698 and 1773 ind m^{-2}, respectively).

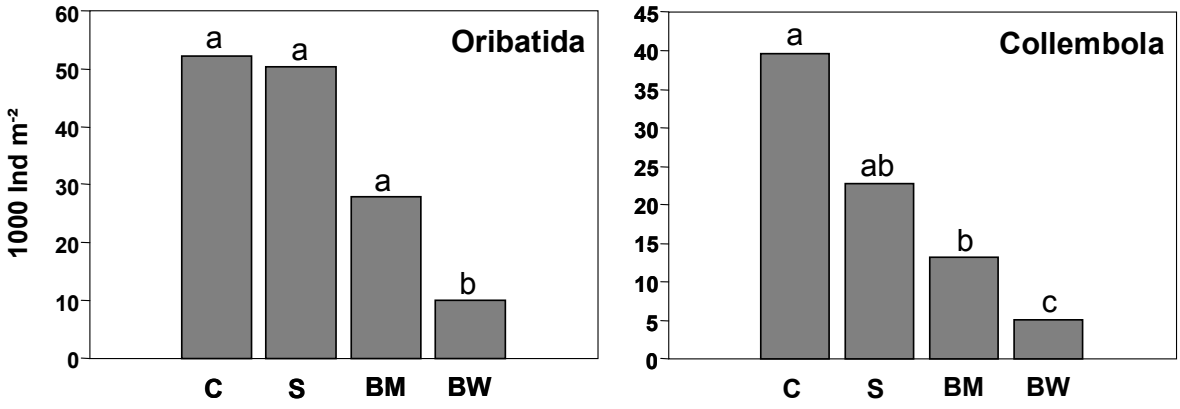

Fig. 2.4.1. Effects of perturbation intensities on the density of oribatid mites and collembolans. **C**, control; **S**, single perturbation; **BM**, perturbation once every two month; **BW**, perturbation once every two weeks. Bars with different letters differ significantly; $P < 0.05$. Back-transformed means of log-transformed data.

MANOVA indicated that oribatid mite groups responded differently to the perturbations (Pillai's Trace, $F_{18,39} = 3.1$, $P < 0.0014$). Subsequent univariate analysis of variance indicated that Enarthronota, Suctobelbidae, Poronota and Oppiidae were affected most ($F_{3,16} = 107.5$, $P < 0.0001$; $F_{3,16} = 15.5$, $P < 0.0001$; $F_{3,16} = 11.8$, $P < 0.0003$; $F_{3,16} = 9.6$, $P < 0.0007$, respectively; Fig. 2.4.2.). In contrast, the density of *Tectocepheus* was not significantly reduced ($F_{3,16} = 0.5$, $P = 0.7$) and the density of Desmonomata was even increased in the single perturbation and the BW perturbation treatments ($F_{3,16} = 11.9$, $P < 0.0002$).

MANOVA of collembolan groups also indicated that collembolan taxa differentially responded to the perturbations (Pillai's Trace; $F_{15,42} = 2.5$, $P < 0.0089$). The density of

Folsomia species was most strongly reduced by perturbation (Fig. 2.4.3.; $F_{3,16} = 37.8$, $P < 0.0001$). Also, the density of Hypogastruridae/Neanuridae, Isotomidae and Onychiuridae was reduced in perturbation treatments ($F_{3,16} = 11.3$, $P = 0.0003$; $F_{3,16} = 8.1$, $P = 0.0017$; $F_{3,16} = 10.3$, $P = 0.0005$, respectively; Fig. 2.4.3.). The density of Entomobryidae was not significantly affected by the treatments ($F_{3,16} = 0.5$, $P = 0.7$; Fig. 2.4.3.). In contrast to oribatid mites, the density of none of the collembolan groups increased in the perturbation treatments.

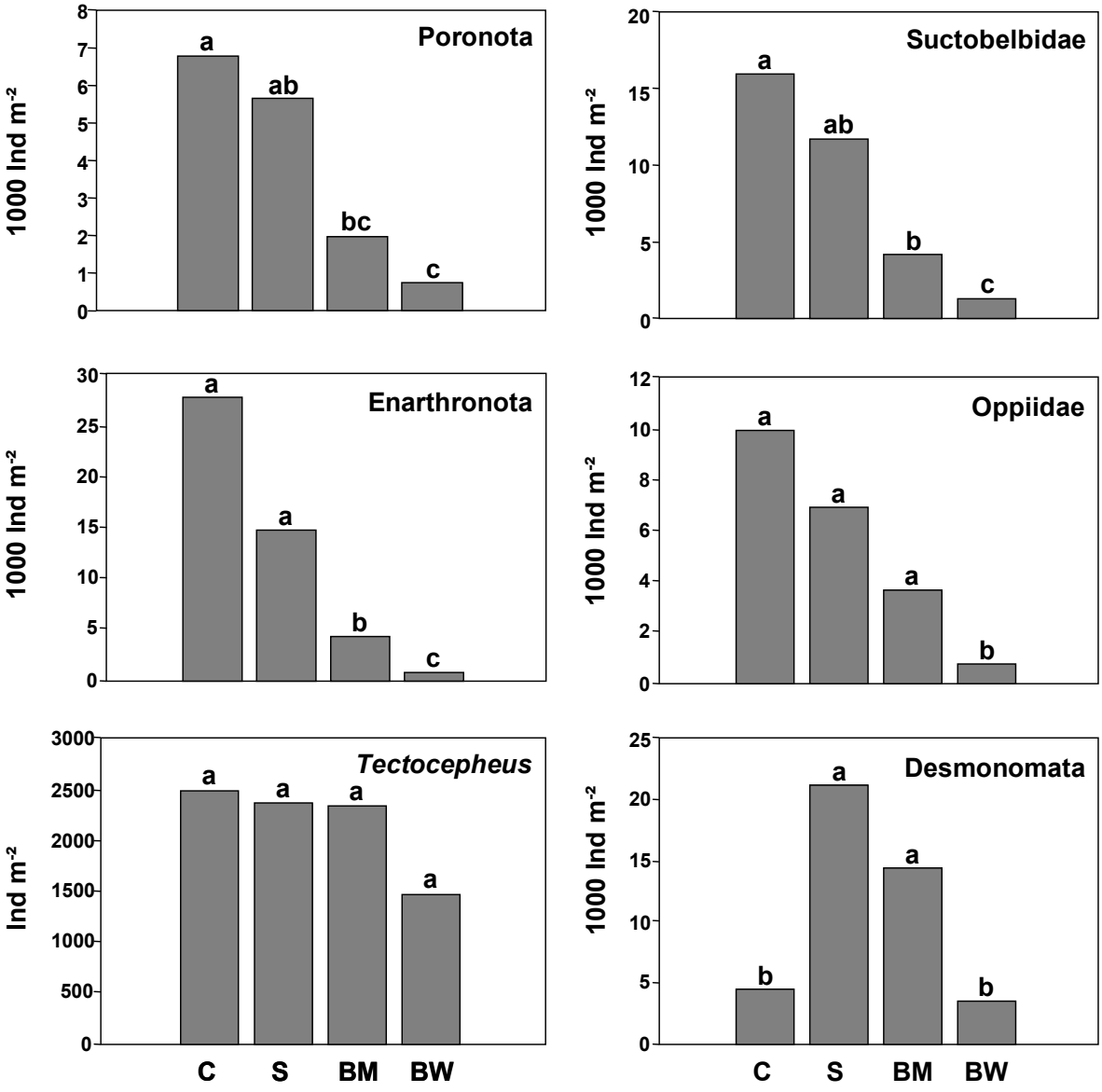

Fig. 2.4.2. Abundance of different groups of oribatid mites after the disturbance (C, control; S, single perturbation; BM, perturbation once every two month; BW, perturbation once every two weeks. Bars with different letters indicate significant differences; $P < 0.05$). Back-transformed data are shown.

The proportion of juvenile oribatid mites significantly increased from 27% in the control to 45% in the single perturbation treatment ($F_{3,16} = 5.3$, $P < 0.01$). In both periodic perturbation treatments the percentages of juveniles was similar (52%) and differed significantly from the control but not from the repeated perturbation treatments (Tukey's HSD test). Most of the juveniles belong to the Desmonomata and their contribution to all juveniles significantly increased from 20% in the control to 54, 67 and 76% in the single, BM and BW perturbation treatments, respectively ($F_{3,16} = 9.3$, $P < 0.001$). Generally, parthenogenetic oribatid mite species dominated (average contribution to the total density of 87%) and their dominance gradually increased from the control (82%) to the strongest (BW) perturbation treatment (91%), however, differences were not statistically significant ($F_{3,16} = 0.8$, $P = 0.52$).

The structure of the microarthropod community

The structure of the oribatid mite and collembolan community differed significantly among treatments (*Wilks' Lambda* = 0.136; approx. $F_{9,34} = 4.8$; $P < 0.0003$). The first axis accounted for 92% and the second axis for 7% of the variation. The control was clearly separated from the other treatments (Table 2.4.1.). The BW perturbation treatment effect was separated from the BM perturbation treatment effect and the single perturbation whereas the BM perturbation and the single perturbation effects were not significantly different.

Table 2.4.1. Squared Mahalanobis distances between group centroids and reliability of the discrimination between the four treatments (**single**, once every two month (**BM**), once every two weeks (**BW**)) for the community structure of microarthropods (oribatid mites and collembolans).

	single	BM	BW
Control	5.2*	7.3*	33.8***
Single perturbation	-	1.6 *ns*	17.7***
BM perturbation		-	10.6**

***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, *ns* not significant

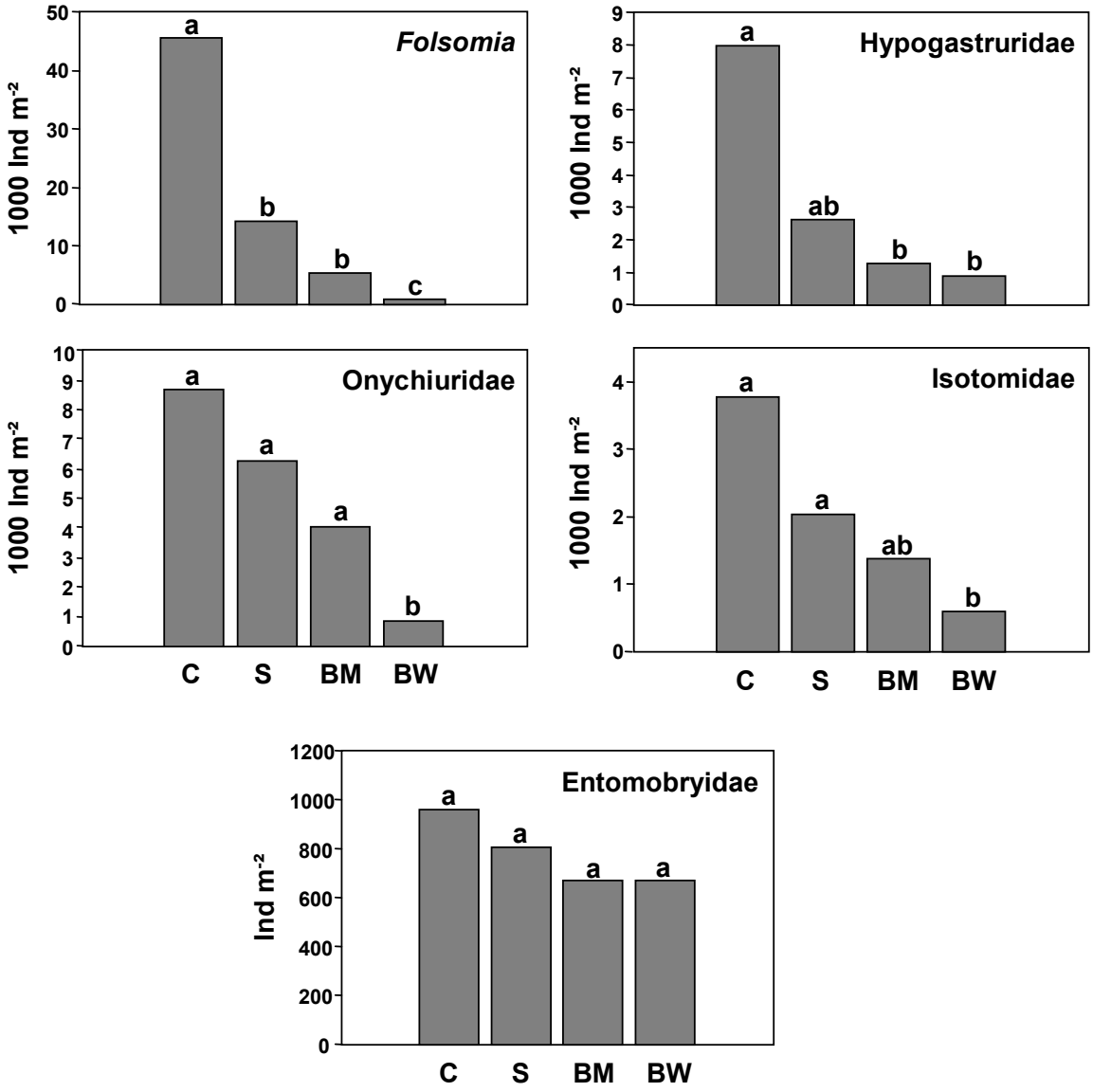

Fig. 2.4.3. Abundance of different groups of collembolans after the disturbance (**C**, control; **S**, single perturbation; **BM**, perturbation once every two month; **BW**, perturbation once every two weeks. Bars with different letters indicate significant differences; $P < 0.05$). Back-transformed data are shown**.**

2.4.5. Discussion

General effect of perturbation

Disturbance is a key process in understanding density and diversity of plant and animal species (Pickett and White 1985). Disturbances include biotic factors, such as predation and competition, and abiotic factors, such as fluctuations of physical factors and catastrophic events. Depending on the intensity of the disturbance the diversity of the organisms may be increased or reduced. Intermediate intensities of disturbance

('intermediate disturbance hypothesis'; Connell and Slatyer 1977, Connell 1978) and intermediate rates of disturbance frequencies ('dynamic equilibrium'; Huston 1979, 1994) have been assumed to maximize species diversity. In contrast to former ideas these models emphasize the importance of non-equilibrium dynamics for maintaining high numbers of species in ecosystems.

Organisms may be subject to disturbances but they may also function as agents of disturbances and affect other organisms in a positive or negative way (metabiosis or engineering; Jones et al. 1994, Waid 1999). In this study I investigated the influence of different rates of disturbance on the community structure of oribatid mites and collembolans of a temperate deciduous forest. It has been assumed that the density, diversity and community structure of oribatid mites and collembolans is strongly influenced by disturbance regimes (Maraun and Scheu 2000).

Our results indicate that disturbances strongly affect the community structure of microarthropods. The density of oribatid mites and collembolans and the diversity of oribatid mites was generally reduced due to disturbances but compared to oribatid mites effects on collembolans were more pronounced indicating that collembolans are more sensitive towards mechanical disturbances. The results also indicate that even low rates of disturbances are detrimental. Therefore, it appears that the intermediate disturbance hypothesis may not apply for soil microarthropods.

Effect of perturbation on oribatid mites

Of the oribatid mites, Poronota, Suctobelbidae and Enarthronota were adversely affected by the mechanical disturbance. These results are in accordance with results from our previous studies (Maraun et al. 1999, Maraun and Scheu 2000, Maraun et al. 2001) in which these groups were found to be very sensitive to disturbance, e.g. due to agricultural management or bioturbation by earthworms. Enarthronota (mainly Brachychthoniidae and

Eniochthonius) lay only few eggs that develop slowly (K-strategists) and therefore recover very slowly after disturbances. Poronota consisted mainly of the taxon *Chamobates*. Individuals of this taxon reproduce sexually and, compared to parthenogenetic reproduction, this may be at a disadvantage in disturbed habitats (Bell 1982). However, some Poronota species, i.e. the genera *Punctoribates* and *Minunthozetes*, increased in numbers following disturbance. These species frequently occur in agricultural systems but reach low densities in forests (Scheu and Schulz 1996). Suctobelbidae were also negatively affected by the disturbances indicating that they should not grouped with Oppiidae that were less affected. However, this aggregation is often done in ecological studies (Madej and Skubala 1996, McLean and Parkinson 2000). Suctobelbidae reproduce more slowly than Oppiidae and this may be the main reason for their low resistance to disturbances. Oppiidae have often been shown to be tolerant of disturbances. The main reasons for this tolerance are probably their opportunistic feeding habits (Stefaniak and Seniczak 1981) and the fast parthenogenetic reproduction of at least some of these species (e.g. *Oppiella nova*; Shereef 1976). Species of the genus *Tectocepheus* were not significantly affected by the disturbances indicating that they are very resistant to mechanical perturbations. This confirms the results of other studies where *Tectocepheus* species have been found to tolerate mechanical disturbances and adverse conditions such as low pH (Hagvar and Amundsen 1981). *Tectocepheus* species reach high densities in disturbed habitats like dolomitic dumps, fields, meadows or heathlands (Schalk 1968, Webb 1994, Skubala 1995, Scheu and Schulz 1996) and are little affected by the presence of earthworms (Maraun et al. 1999). One of the main reasons for their resistance to disturbance may be their parthenogenetic mode of reproduction.

Interestingly, Desmonomata increased in response to the single and BM perturbations. Even in the stronger BW perturbation treatment their density was similar to that in the control. The main reason for the high density of Desmonomata was the large number of

juveniles in the disturbed plots. In the single perturbation treatment 50% of all juveniles of oribatid mites were Desmonomata and in the periodic perturbation plots 65% of the juveniles were Desmonomata. These results confirm that Desmonomata are able to reproduce very quickly after disturbances (Travé et al. 1996) and this may explain why juvenile Desmonomata are present at disturbed sites (Hülsmann and Wolters 1998). However, in contrast to Oppiidae, *Tectocepheus* and some species of Poronota, Desmonomata do not reach high densities at disturbed sites indicating that they are weak competitors when other oribatid mites are present. Only under the strong artificial disturbances employed in this experiment did their densities exceed those of the other oribatid mite species. As for *Tectocepheus*, Desmonomata may have been more able to proliferate from their parthenogenetic mode of reproduction.

Effect of perturbation on collembolans

Among Collembola the taxa *Folsomia* and Hypogastruridae/Neanuridae were most affected by disturbance but Onychiuridae and Isotomidae also declined in the disturbed plots. In contrast, the density of Entomobryidae was not significantly reduced in disturbed plots. The most abundant *Folsomia* species was *F. quadrioculata* (J.-A. Salamon, pers. comm.) which reproduces sexually (A. Fjellberg, unpubl. MSc, University of Bergen, 1974; V. Wolters, unpubl. PhD Thesis, University of Göttingen, 1985). Interestingly, the dominance of *F. quadrioculata* in the Göttinger Wald, a mull forest with high earthworm density, is low (26%; V. Wolters, loc. cit.) compared to 72% in the undisturbed control of the Solling and 51% in the single perturbation plots. Experimental stimulation of earthworm activity in the Göttinger Wald has been shown to further reduce the density of *Folsomia* and Hypogastridae/Neanuridae (Maraun et al. 2001). Other studies also confirm the sensitivity of *Folsomia* species to disturbances (Birkemoe and Somme 1998). Onychiuridae were adversely affected by disturbance. The reduced density of

Onychiuridae is not surprising since Onychiuridae avoid disturbed microsites such as earthworm middens (Maraun et al. 1999) and also sites with high numbers of earthworms (Maraun et al. 2001).

The density of Isotomidae was not significantly reduced in the single perturbation treatments, indicating that these species are adapted to moderate amounts of disturbances. Some species of Isotomidae, like *Isotoma notabilis* and *I. minor*, reproduce by parthenogenesis and often have several generations per year (Massoud 1971, Petersen 1971, 1980, Greenslade and Greenslade 1980, Hutson 1981). Interestingly, dominance of Isotomidae was 1% in the control treatment and increased to 9% in the single perturbation treatment, becoming similar to that in the Göttinger Wald (24%; V. Wolters, loc. cit.). Also, it has been shown that the density of *Isotoma violacea* in earthworm middens is increased compared with the surrounding soil (Maraun et al. 1999). Kopeszki and Meyer (1994) found high densities of Isotomidae due to increasing intensities of disturbance whereas the density of *Folsomia quadrioculata* decreased with increasing earthworm activity. Additionally, Tiunov and Kuznetsova (2000) found densities of *Isotoma notabilis* and *Isotomiella minor* to be increased in earthworm burrows in a lime forest while that of *Isotoma viridis* decreased. Marinissen and Bok (1988) also reported high densities of *Isotoma notabilis* in grasslands with high earthworm densities.

The ‘intermediate disturbance hypothesis’

Scheu and Schulz (1996) speculated that, consistent with the intermediate disturbance hypothesis, moderate earthworm activity might increase the diversity of soil microarthropods in the long term because intermediate amounts of disturbance reduce the strength of biotic interactions such as competition. However, our results indicate that the intermediate disturbance hypothesis does not apply to soil microarthropods. It is tempting to speculate that soil microarthropod communities in forest ecosystems are close to

equilibrium conditions. For a moder forest, such as the Solling, the results of our study indicate that they are in fact close to equilibrium conditions because disturbing agents such as earthworms are virtually absent. I therefore postulate that in forests with moder type humus competition between species of soil microarthropods is intense and resources are limiting. In contrast, forests like the Göttinger Wald with calcareous soils, where earthworm density is high and disturbances due to their burrowing activity is intense, the soil microarthropod community is likely to be far from equilibrium and competition between soil microarthropods of limited importance.

Appendix

Taxonomic composition of oribatid mites as used for the multivariate analysis of variance (MANOVA).

Oribatid mites: Poronota: *Hemileius initialis*, *Scheloribates pallidulus*, *Adoristes ovatus*, *Chamobates voigtsi*, *C. borealis*, *C. cuspidatus*, *Eupelops plicatus*; Suctobelbidae: *Suctobelba* spec., *Suctobelbella* spec.; Enarthronota: *Hypochthonius rufulus*, *Eniochthonius minutissimus*, Brachychthoniidae; Oppiidae: *Oppiella nova*, *O. ornata*, *O. subpectinata*, *O. splendens*, *O. sigma*, *Oppiella* spec.; Tectocepheus: *Tectocepheus* spp.; Desmonomata: *Nothrus silvestris*, *Platynothrus peltifer*, *Nanhermannia nana*, *N. coronata*

2.5. Transitory dynamics in the soil invertebrate community of a temperate deciduous forest: effects of resource quality

2.5.1 Abstract

The importance and strength of bottom-up forces in soil systems are poorly understood. In contrast to aquatic systems, where trophic cascades and top-down forces dominate, it has been postulated that terrestrial systems are regulated mainly by bottom-up forces. We set up a 17 month field experiment to study the effects of addition of resources of different quality (wood, wheat bran, pet food, and glucose + phosphorous + nitrogen) on the soil micro-, meso- and macrofauna as well as on microbial biomass, ergosterol content and abiotic parameters (soil pH, water content, carbon and nitrogen content) in a beech forest (*Fagus sylvatica*) on sandstone. We hypothesized that bottom-up effects will be strong at lower trophic levels resulting in increased biomass of bacteria and fungi, and that this increase will propagate to higher trophic levels (microbivorous invertebrates, predators) but with decreasing intensity due to dampening of bottom-up forces at higher trophic levels by high connectivity, trophic-level-omnivory and generalist feeding. The results of the study in general did not support these hypotheses. Microbial biomass only moderately increased after resource addition, and while densities of several animal groups increased (lumbricids, collembolans, gamasid mites, staphylinid beetles), densities of other groups declined (oribatid mites, prostigmate mites, lithobiids), and a large number of taxa remained unaffected (enchytraeids, diplopods, uropodine mites, pseudoscorpions, spiders). We conclude that (a) bottom-up forces are of limited importance in the soil system of temperate deciduous forests, (b) large primary decomposers, such as earthworms, do not depend on microorganisms as food but consume organic matter directly, (c) the link between microorganisms and microbivores, such as collembolans, is weak since

collembolan density increased even though microbial biomass was unaffected, (d) habitat modification by ecosystem engineers, such as earthworms, is more important than resource availability for a number of soil invetebrates including oribatid mites and prostigamte mites, and (e) the soil food web in general is rather resistant responding little to changes in resource supply.

2.5.2 Introduction

Both bottom-up and top-down forces are structuring animal and plant communities but it is debated which of these forces predominate in ecological systems and how strong they are (McQueen et al. 1989, Hunter and Price 1992, Peterson et al. 1993, Moran and Scheidler 2002). It is also disputed how far up in the food chain bottom-up effects extend and how strong effects from the top influence trophic levels at the base of the food web (Hunter and Price 1992, Menge 1992, Power 1992, Strong 1992, Halaj and Wise 2001). It has been proposed that in aquatic systems top-down forces predominate forming trophic cascades (Paine 1980, 1988, Carpenter et al. 1985) where predators function as indirect mutualists for food organisms of their prey (Schoener 1993, Menge 1995, Schmitz et al. 1997, Persson 1999). Alterations at high trophic levels may be transferred to lower trophic levels without reduction in intensity (Townsend 2003).

Trophic cascades also occur in terrestrial systems (Spiller and Schoener 1990, Hunter and Price 1992, Strong 1992, Schmitz et al. 1997) including species-poor agricultural systems (Riechert and Bishop, 1990) but also complex and species-rich systems, such as temperate and tropical forests (Altegrim 1989, Letourneau and Dyer 1998) and soil communities (Strong et al. 1999). However, compared to aquatic systems, bottom-up forces appear to dominate in terrestrial systems (White 1978, Polis 1994, Polis and Strong 1996). Due to intraguild predation, omnivory and high connectivity terrestrial food webs buffer cascading effects (Polis 1991, Hunter and Price 1992, Strong 1992, Mikola and

Setälä 1998, Halaj and Wise 2002) and result in 'trophic trickles' rather than trophic cascades (Strong 1992, Halaj and Wise 2001, Dawes-Gromadzki 2002, Dyer and Letourneau 2003).

In below-ground systems, bottom-up forces appear to dominate (Ponsard et al. 2000), however, few studies have investigated if resources or consumers are more important (Slobodkin et al. 1967, Heal and Dighton 1985, Hunt et al. 1987). The main argument for the dominance of the resource control is that litter does not accumulate and therefore the systems need to be bottom-up controlled (Hairston et al. 1960). However, this argument is only valid for saprophytic bacteria and fungi and for animals that feed directly on decomposing litter (Anderson and Domsch 1978, Wardle 1992, Gallardo and Schlesinger 1994); it does not apply for animals feeding on bacteria, fungi and algae or for higher level consumers. Bottom-up forces have been reported to structure the density and community structure (=species richness and dominance) of some groups of the soil macrofauna in a mull beech forest (Göttinger Wald, Germany; Scheu and Schaefer 1998) but not to affect the density and community structure of the soil mesofauna in the same experiment (Maraun et al. 2001). Presumably, the increase in earthworm density indirectly affected the soil mesofauna via competition for resources and habitat destruction in that experiment (Maraun et al. 2003b). These effects of large ecosystem engineers, such as earthworms, alter the whole soil food web and may override bottom-up and top-down forces. Therefore, we set up an experiment in an acidic beech forest where earthworms are scarce to avoid the possibility that experimentally increased density of these large detritivores overrides trophic responses. By adding resources with different nitrogen content we investigated the role of resource quality for controlling the soil invertebrate community. The resources included wood, a mixture of glucose, nitrogen and phosphorous, pet food and wheat bran ranging in C-to-N ratio from 1080 to 18. A shortcoming of bottom-up experiments is often the way in which resources are added. If resources are added as particulate materials (Judas

1990, Chen and Wise 1997) the amount of resources is increased but also the size of habitable space, making the separation of these two effects difficult. We therefore added the resources as powder which was dissolved in water to minimize habitat changes and hypothesized that resources with high C-to-N ratios will predominantly promote the fungal food chain, whereas resources with low C-to-N ratios will predominantly promote the bacterial food chain. We investigated the response of the three major components of the soil food web to the addition of resources: microorganisms, animal decomposers (Lumbricidae, Diplopoda, Collembola, Oribatida) and predators (Staphylinidae, Aranaeida, Lithobiidae, Pseudoscorpionida, Prostigmata, Uropodina, Gamasina).

2.5.3. Materials and Methods

Study site

The study site is located 50 km northwest of Göttingen in the Solling forest, a 135 yr old beech forest (*Fagus sylvatica* L.) in Lower Saxony (Germany). In the forest the herb layer is poorly developed and consists mainly of *Luzula luzuloides, Avenella flexuosa, Oxalis acetosella* and *Polytrichum* mosses (Ellenberg et al. 1986). The Solling is a mountain range of about 400 km² at 500 m a.s.l. Parent rock is red sandstone which at the study site is covered with a loess layer of about 1 m. The soil type is an acidic Cambisol with the humus form moder. Litter and soil pH are low (3.0 and 3.4, respectively). The average annual precipitation is 1045 mm and the average annual temperature is 6.5 °C (Ellenberg et al. 1986). The experiment was conducted at a fenced site where trees have not been harvested during the last 40 years.

Experimental design and sampling

In April 1997 circular experimental plots of 1 m² were established in the forest using plastic fences of 40 cm height. The fences were dug into the soil to a depth of 5 cm. Five

treatments were established: watered control (ctr), wood, CNP (addition of carbon, nitrogen and phosphorous), pet food (pf) and wheat bran (wb). The CNP medium consisted of glucose, NH_4NO_4 and NaH_2PO_4 dissolved in 6 l of deionised water. The amount of C, N and P in the CNP solution added was equivalent to five times the annual litter input (1120g C, 36g N, 2g P). The organic materials (wood, wheat bran, pet food) were dried and milled to a powder. They were added to 6 l of deionised water and the solution was added every second week. The amount of the organic materials added was equivalent to five times the weight of the annual litter input (1900 g dw m^{-2}). The C-to-N ratio of the materials increased in the order wheat bran (18), pet food (22), CNP (31) and beech wood (1080). The control plot was irrigated every second week with 6 l of deionised water. The total amount of water added to each plot was equal to ca. a quarter of the annual precipitation. Each treatment was replicated five times. The plots were arranged in blocks in a randomised complete blocks design. The experiment started in April 1997 and lasted for 17 month.

At the end of the experiment, in September 1998, four soil cores (∅ 5 cm) were taken from each experimental plot and separated into three horizons (L/F, H/Ah and 0-3 cm of Bv). The material of three cores was mixed and sieved (4 mm) and used for measuring soil moisture, soil C and N, microbial biomass and respiration. Soil microarthropods were extracted from the fourth soil core by heat (Macfadyen 1961). An additional soil core (∅ 21 cm) was taken from each plot for extracting soil macrofauna (Kempson et al. 1963).

Soil moisture content was determined gravimetrically after drying at 105°C for 24 h. The content of C and N in litter and soil materials was determined from dried and powdered samples using an elemental analyser (Carlo Erba, Milan, Italy). Microbial respiration was measured using an automated respirometer based on electrolytic O_2 microcompensation (Scheu 1992). Basal respiration was measured in fresh litter and soil materials equivalent to 5 g dry wt by averaging respiration rates of hours 10-20 after start

of the measurements. Microbial biomass was calculated from the maximum initial respiratory response (MIRR; μgO_2/g dry wt h) following glucose addition (substrate induced respiration method; Anderson and Domsch 1978) of fresh soil samples equivalent to 2 g dry wt. Microbial carbon was calculated as 38.0 x MIRR (Anderson and Domsch 1978, Beck et al. 1997) from oxygen uptake of soil samples supplemented with 8,000 µg glucose (g dry wt)$^{-1}$ and litter samples supplemented with 80,000 µg glucose (g dry wt)$^{-1}$ assuming a respiratory quotient of 1.0 (cf. Ross 1980). Glucose was added as a solution to increase the water content to 100 % of dry wt (cf. Cheng and Coleman 1989, Theenhaus et al. 1997). Using data on microbial biomass and basal respiration the specific respiration (µg O_2 mg^{-1} C_{mic} h^{-1}) was calculated (cf. Anderson and Domsch 1990). Ergosterol was measured according to Djajakirana et al. (1996); in brief, from each sample 1 g fresh wt was extracted with 100 ml ethanol for 30 min by oscillating shaking at 250 rev min^{-1}. Subsequently, quantitative determination of ergosterol was performed by Rainer G. Joergensen at the University of Kassel (Faculty of Organic Agricultural Sciences in Witzenhausen) by reversed-phase HPLC analysis at 25°C using a column of 12.5 cm Spherisorb ODS II S5 with a mobile phase of 97% methanol / 3% water (v/v) and detection at 282 nm.

The invertebrate taxa were determined by several authors: Oribatid mites (on species level, except Brachychthoniidae, Phthiracaridae, Suctobelbidae, Carabodes spp., Brachypylina juvenile), prostigmate mites and Uropodina by myself; Gamasina by A. Ruf (Bremen); Aranaeida, Pseudoscorpionida, Lithobiidae and Staphylinidae by A. Sührig (Göttingen); Collembola, Diplopoda and Lumbricidae by J.-A. Salamon (Gießen). Oribatid mites were determined to species level whenever possible.

Statistical analysis

Abundances of invertebrate taxa, microbial biomass and respiration, and abiotic variables were analysed by multivariate analysis of variance (MANOVA, *Wilks' Lambda*; Scheiner and Gurevitch 2001), using SAS 8e (SAS Institute Inc., Cary, USA). The factors analysed were 'resource addition' (ctr, wood, CNP, pf, wb) and 'block'; however, due to limited effects of 'block' it was excluded from the final statistical analysis of the data. To estimate which of the factors contributed most to the MANOVA effects, we performed separate univariate analyses of variance (protected ANOVAs; Scheiner and Gurevitch 2001) for invertebrate taxa, microbial parameters and abiotic variables. All data were log-transformed prior to ANOVAs to increase homogeneity of variances and Tukey`s honestly significant differences were calculated for comparison of means (Sokal and Rohlf 1995).

Separate MANOVA was performed for oribatid mites. For this analysis oribatid mites were separated into seven taxonomic groups (Enarthronota, Desmonomata, Mixonomata, *Tectocepheus*, Oppiidae, Suctobelbidae, Poronota; see Appendix). To estimate which oribatid mite group contribute most to the MANOVA effect, we analysed separate univariate analyses of variance (protected ANOVAs; Scheiner and Gurevitch 2001) for all groups. Additionally, we performed a univariate analysis of variance for species when the ANOVAs for the respective taxonomic groups were significant. The diversity of oribatid mites (species number, Shannon-Wiener index, Eveness) was investigated using analysis of variance (ANOVA) with the factor 'resource addition' (ctr, wood, CNP, pf, wb).

Discriminant function analyses (DFA) with log-transformed microbial and abiotic data and also with invertebrate densities were conducted to evaluate if the plots grouped according to the treatments. Squared Mahalanobis distances between group centroids were calculated to test for significant differences between the five resource treatments. DFA was implemented using STATISTICA 5.0 (Statsoft Inc., Tulsa, USA).

2.5.4. Results

Abiotic factors

The abiotic variables studied significantly differed between the five resource treatments (MANOVA; *Wilks' Lambda*, $F_{7,17} = 21.7$, $P < 0.0001$). Protected ANOVAs for each of the abiotic variables indicated that soil N content in the wood treatment was significantly lower than in the other treatments (Fig. 2.5.1., Table 2.5.1.). The other abiotic variables measured (C content, pH, soil moisture, height and weight of the organic layer) were not significantly affected by the experimental treatments (Table 2.5.1.).

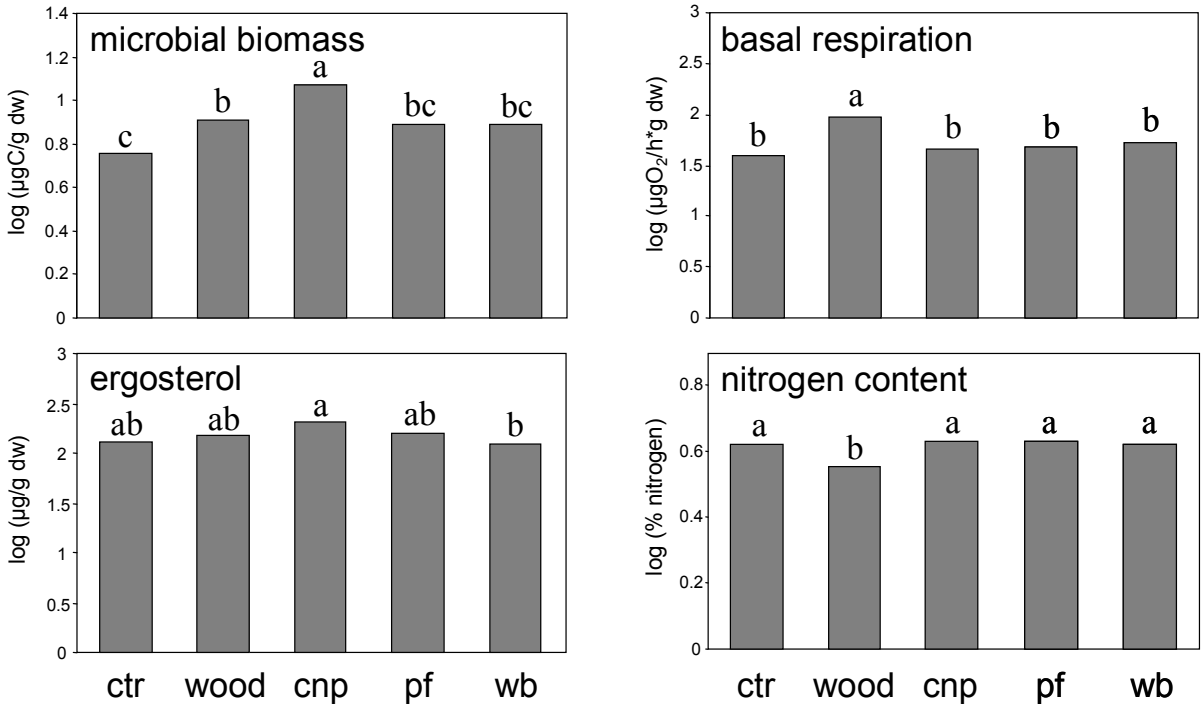

Fig. 2.5.1. Response of microorganisms (microbial biomass, basal respiration, ergosterol) and nitrogen content (log-transformed data, mean of the three horizons) in soil of the Solling forest to the addition of resources of different quality (**ctr**, control; **CNP**, carbon+nitrogen+phosphorous; **wood**, wood powder; **wb**, wheat bran; **pf**, pet food). Bars with different letters are significantly different (Tukey's HSD, $P < 0.05$).

Response of microorganisms

Microorganisms significantly responded to resource additions (Table 2.5.1.). Protected ANOVAs indicated that the response of basal respiration and microbial biomass was more pronounced than that of fungi measured as ergosterol content (Fig. 2.5.1., Table 2.5.1.).

Compared to the control, microbial biomass was significantly increased in CNP and wood treatment while basal respiration was significantly increased in the wood treatment only. Ergosterol concentrations differed only between CNP and wheat bran teatment, with CNP having a higher value (Fig. 2.5.1.).

Table 2.5.1. MANOVA table of F values (*Wilks' Lambda*) on the effect of resource addition on soil invertebrate taxa (**A**), microorganisms (**B**) and abiotic parameters (**C**), and F values of the 'protected ANOVAs' for the response of the animal taxa, microbial parameters and abiotic parameters studied.

	F values					
A)	*df*			**B)**	*df*		
MANOVA:				MANOVA:			
Wilks' Lambda	33,52	3.9	***	*Wilks' Lambda*	12,48	47.9	***
protected ANOVAs:				protected ANOVAs:			
primary and secondary decomposers				microbial biomass	4,24	11.7	***
Lumbricidae	4,24	11.2	***	basal respiration	4,24	14.2	***
Diplopoda	4,24	1.1		ergosterol content	4,24	3.1	*
Collembola	4,24	12.7	***				
Oribatida	4,24	3.6	*	**C)**			
predators				MANOVA:			
Staphylinidae	4,24	6.9	**	*Wilks' Lambda*	28,52	2.1	**
Lithobiidae	4,24	5.5	**	protected ANOVAs:			
Aranaeida	4,24	0.4		C content	4,24	0.3	
Pseudoscorpionida	4,24	2.2		N content	4,24	5.4	**
Prostigmata	4,24	6.1	**	C to N ratio	4,24	5.4	**
Gamasina	4,24	13.2	**	pH	4,24	0.9	
Uropodina	4,24	2.3		water content	4,24	0.5	
				sample height (cm)	4,24	0.5	
				sample weight	4,24	0.2	

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Response of soil invertebrates

Some invertebrate taxa were affected by resource additions as indicated by MANOVA (Table 2.5.1.). Overall, densities of four of the eleven higher taxa were increased (Lumbricidae, Staphylinidae, Gamasina, Collembola), three were declined (Lithobiidae, Prostigmata, Oribatida) and four were not significantly affected (Uropodina, Pseudoscorpionida, Diplopoda, Aranaeida) by resource additions (Table 2.5.1.).

Primary and secondary decomposers

Total density of oribatid mites was slightly reduced in the resource addition treatments except in the CNP treatment. The strongest reduction occurred in the pet food treatment (Fig. 2.5.3., Table 2.5.1.). Two oribatid mite groups, Enarthronota and Poronota, significantly responded to resource treatments (Table 2.5.2.). Enarthronota had low densities in the wheat bran and pet food treatment whereas Poronota had low densities in the wheat bran and wood treatment. The reduced densities in Enarthronota and Poronota were mainly due to Brachychthoniidae and Chamobatidae, respectively (Fig. 2.5.2.). In contrast, the diversity of oribatid mites (species number, Shannon-Wiener index, Eveness) was not significantly affect by resource addition ($F_{4,24} = 2.08$, $P = 0.12$; $F_{4,24} = 0.66$, $P = 0.62$; $F_{4,24} = 0.31$, $P = 0.87$, respectively). The total density of collembolans was reduced by the wood and enhanced by the pet food treatment (Fig. 2.5.3., Table 2.5.1.). In contrast the density of Lumbricidae was significantly higher in the pet food and wheat bran treatment than in the control (Fig. 2.5.3., Table 2.5.1.).

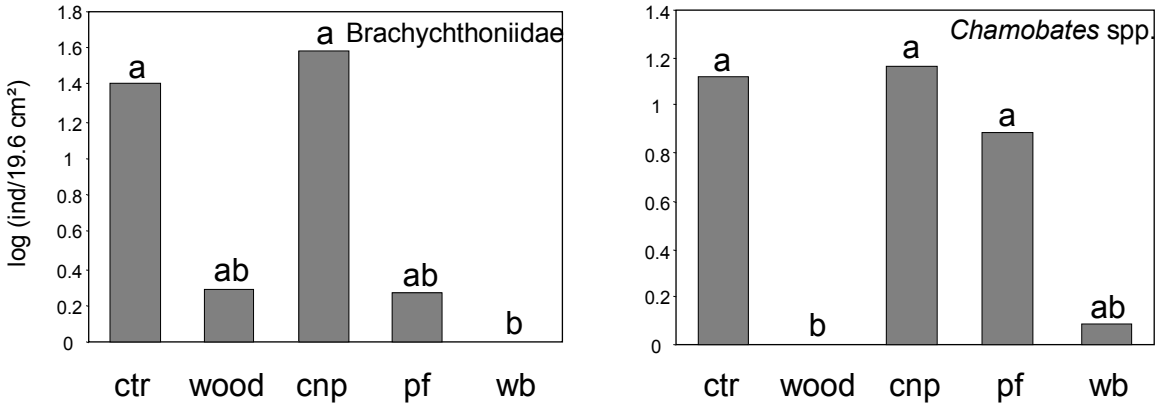

Fig. 2.5.2. Response of oribatid mites taxa (Brachychthoniidae and *Chamobates* spp.; log-transformed data) in soil of the Solling forest to the addition of resources of different quality (**ctr**, control; **CNP**, carbon+nitrogen+phosphorous; **wood**, wood powder; **wb**, wheat bran; **pf**, pet food). Bars with different letters are significantly different (Tukey's HSD, $P < 0.05$).

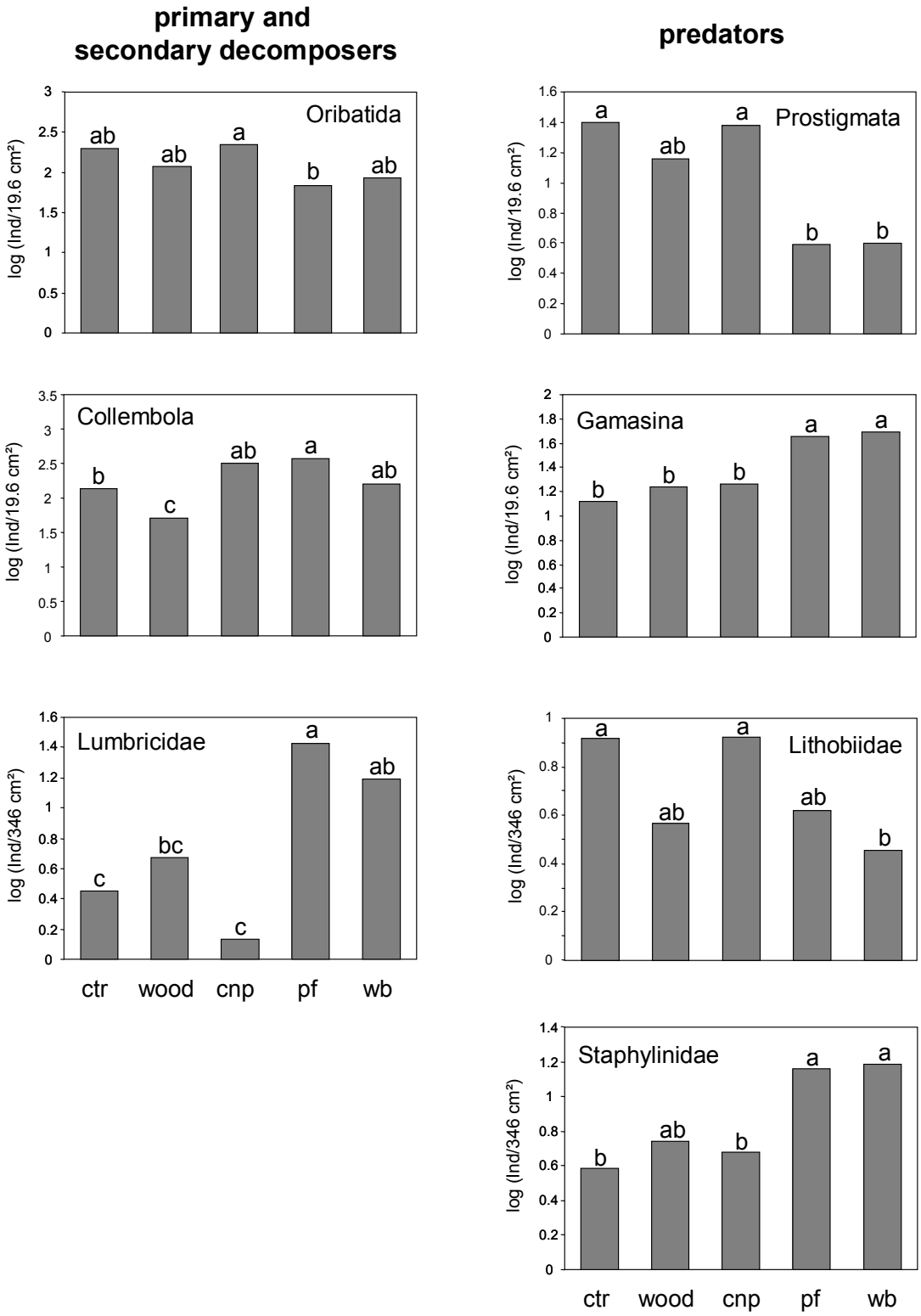

Fig. 2.5.3. Response of invertebrate taxa (log-transformed data) in soil of the Solling forest to the addition of resources of different quality (**ctr**, control; **CNP**, carbon + nitrogen + phosphorous; **wood**, wood powder; **wb**, wheat bran; **pf**, pet food). Bars with different letters are significantly different (Tukey's HSD, $P < 0.05$).

Table 2.5.2. MANOVA table of F values (*Wilks' Lambda*) on the effect of resource addition on Oribatida and F values of 'protected ANOVAs' for the response of the subgroups of Oribatida.

	df	*F-value*
MANOVA:		
Wilks' Lambda	24,53	2.2 **
protected ANOVAs:		
Enarthronota	4,24	2.8 *
Desmonomata	4,24	1.8
Tectocepheus	4,24	0.7
Suctobelbidae	4,24	1.5
Oppiidae	4,24	1.4
Poronota	4,24	7.3 ***

**P < 0.05, **P < 0.01, ***P < 0.001*

Predators

When compared to control, density of Staphylinidae was increased by the wheat bran and pet food treatments (Fig. 2.5.3., Table 2.5.1.). In contrast the density of Lithobiidae was strongly reduced in wheat bran treatment (Fig. 2.5.3., Table 2.5.1.). Densities of prostigmate mites were also reduced by the wheat bran and pet food treatments (Fig. 2.5.3., Table 2.5.1.). Similar to Staphylinidae, the total density of Gamasina was significantly increased by the wheat bran and pet food treatments (Fig. 2.5.3., Table 2.5.1.).

Discriminant function analysis

Based on the abiotic and microbial parameters, discriminant function analysis (DFA) significantly separated the resource treatments (*Wilks' Lambda* = 0.0006, $F_{40,44} = 5.4$, $P < 0.0001$), with the first axis accounting for 83% and the second for 13% of the variation. The CNP and the wood treatments differed significantly from each other and from all other treatments, while control, pet food and wheat bran treatments did not significantly differ from each other (Fig. 2.5.4., Table 2.5.3.).

Based on the density of the invertebrate taxa, DFA also significantly separated the resource treatments (*Wilks' Lambda* = 0.0006, $F_{33,52} = 3.5$, $P < 0.0001$), with the first axis accounting for 60% and the second for 36% of the variation. In contrast to the DFA of abiotic and microbial parameters, the control did not differ from the CNP and wood treatments but instead from the wheat bran and pet food treatments. Wood and CNP treatments differed from the wheat bran and pet food treatments and from each other, while the pet food and wheat bran treatment did not differ from each other (Fig. 2.5.5., Table 2.5.4.).

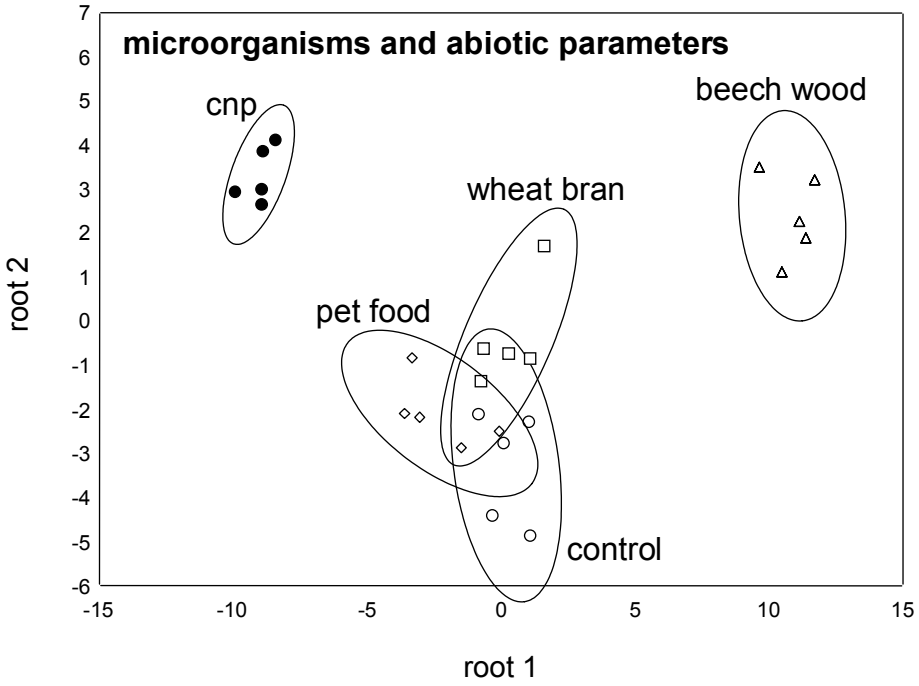

Fig. 2.5.4. Separation of resource treatments (**cnp**, carbon+nitrogen+phosphorous) by discriminant function analysis (DFA) according to microorganisms. Ellipses represent 95% confidence limits.

Table 2.5.3. Squared Mahalanobis distances between group centroids and reliability of the discrimination between the five resource treatments for microbial and abiotic parameters.

	CNP	wood	wheat bran	pet food
control	162.2 ***	184.4 ***	22.9	16.3
CNP	-	497.2 ***	133.4 ***	96.6 ***
wood		-	156.3 ***	243.4 ***
wheat bran			-	17.9

****P < 0.001, **P < 0.01, *P < 0.05*

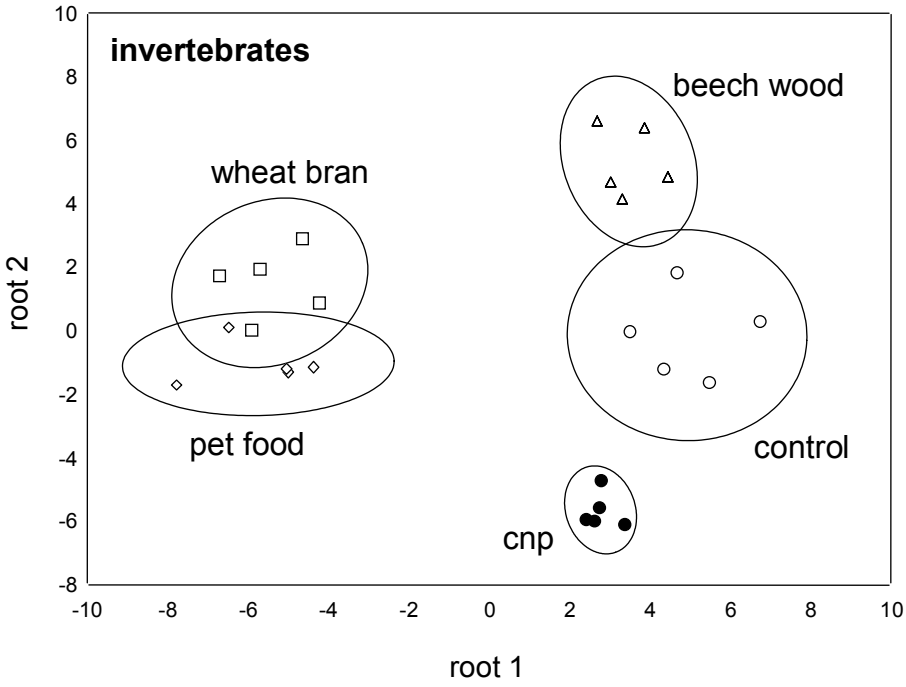

Fig. 2.5.5. Separation of resource treatments (**cnp**, carbon+nitrogen+phosphorous) by discriminant function analysis (DFA) according to invertebrate densities. Ellipses represent 95% confidence limits.

Table 2.5.4. Squared Mahalanobis distances between group centroids and reliability of the discrimination between the five resource treatments for the community structure of soil invertebrates.

	CNP	wood	wheat bran	pet food
control	48.5	44.0	145.8 **	142.8 **
CNP	-	151.7 **	149.9 **	122.2 **
wood		-	121.3 **	159.7 **
wheat bran			-	17.4

****P < 0.001, **P < 0.01, *P < 0.05*

2.5.5. Discussion

Microorganisms

Microorganisms significantly responded to the addition of resources, however, considering the large quantity of resources added, their response was rather limited. A five-fold increase in resources (compared with the average annual input) significantly increased the microbial biomass in the CNP and wood treatment only. Presumably, the increase in the CNP treatment was mainly due to fungi as indicated by the high ergosterol content. Microbial biomass in the wheat bran and pet food treatment was also increased but this increase was not associated with an increase in ergosterol content suggesting that it was caused by bacteria. Basal respiration and microbial biomass were higher in the wood treatment but ergosterol content was not affected. This was unexpected since fungi are the main decomposers of lignin and cellulose (Dix and Webster 1995). Overall, however, the results suggest that the microbial community is surprisingly resistent to variations in quantity and quality of resource inputs, a phenomenon which has been stressed previously by Joergensen and Scheu (1999) and Wardle (2002). There are three possible explanations for this. First, resources may have been consumed in large by saprophagous soil invertebrates thereby effectively competing with soil microorganisms. Second, microbial feeding soil animals may have limited the growth and reproduction of fungi and bacteria via grazing and, third, microorganisms may only in part be limited by carbon and nutrients, and other factors, such as habitable space (surface area of organic matter and minerals), may be more important.

The aim of our experiment was to increase the amount of microorganisms that are available as food for the higher trophic levels to explore to what extent bottom-up effects propagate through the food web. We achieved this goal but the increase in microbial biomass was smaller than expected. Other studies that have investigated the importance of bottom-up effects did not measure microbial biomass after the addition of resources

(Müller et al. 1993, Chen and Wise 1997). For instance, Chen and Wise (1997) added sliced mushrooms, potatoes and dry instant *Drosophila* medium to the litter horizon of a deciduous forest to test the hypothesis that populations of fungivorous arthropods in the forest litter are food limited. The results supported their hypothesis but it remained unclear if the response of the soil invertebrates was based on increased bacterial or fungal biomass or if they benefited directly from feeding on the organic materials.

Primary and secondary decomposers

Oribatid mites generally did not benefit from resource additions. In a previous experiment in a beechwood on limestone, oribatid mites neither responded to the addition of resources (CNP) (Maraun et al. 1999, 2003b). However, in this study it was not possible to separate effects caused by addition of resources and indirect effects due to increased density of earthworms. In the present experiment, earthworm densities also increased in the pet food and wheat bran treatment and this may have detrimentally affected oribatid mites (Maraun et al. 1999). Indeed, the density of Brachychthoniidae which are sensitive to perturbations (Maraun et al. 2003b) significantly decreased in the wheat bran treatment.

Collembolan density increased in the pet food treatment, while microbial biomass did not increase, suggesting that collembolans directly fed on the pet food. This resembles the response of collembolans in the food-enhancement experiments of Chen and Wise (1997, 1999) and Halaj and Wise (2002). Collembola generally do not feed on food resources rich in cellulose and lignin (Hurej et al. 1992) and this may explain why they did not respond to the addition of wheat bran and beech wood. Overall, the results indicate that collembolans are limited by the amount of high quality food, but not necessarily by the availability of microorganisms.

Earthworm densities strongly increased in the wheat bran and pet food treatments. These findings support the views that earthworms are bottom-up limited (Grossmann et al.

1990, Scheu and Schaefer 1998) and that resources are more important than soil pH in controlling earthworm populations (Grossmann et al. 1990). Moreover, as soil pH did not respond to the resource treatment, earthworms appear to have benefited directly from the wheat bran and pet food added instead of relying on increased microbial biomass.

Predators

Application of wheat bran and pet food significantly increased numbers of staphylinid beetles. In the pet food but not in the wheat bran treatment this increase was associated with inceased numbers of collembolans suggesting that in addition to collembolans also other prey species contributed to this response.

Although Lithobiidae are known to feed on collembolans and earthworms (Albert 1983), the density of Lithobiidae was reduced in the wheat bran food treatment where earthworms flourished. Similar to oribatid mites, densities of lithobiids may have been reduced due to disturbances by the burrowing and feeding activities of earthworms as has been concluded in a previous experiment (Scheu and Schaefer 1998).

Prostigmata probably not only feed on invertebrate prey but also on microorganisms (Walter and Proctor 1999). As the density of Prostigmata declined in pet food and wheat bran treatments Prostigmata may also have suffered from habitat destruction by earthworms.

Population density of Gamasina was significantly increased in the two high quality resource treatments, pet food and wheat bran. Karg (1983) found predatory mite population to be coupled tightly to nematode prey in the field. Indeed, the density of Nematoda also increased in the wheat bran treatment (Salamon et al. 2005) These results indicate that bottom-up effects propagated into the predator level.

Reconsidering the importance of bottom-up control

Results of this study suggest that the availability of food resources, i.e. bottom-up control, is of minor importance as a structuring force of soil invertebrate communities. Only few decomposer taxa responded to increased resource input and the effects only occasionally propagated into predators. Several factors may have interferred with bottom-up forces and led to a dampening of bottom-up effects at higher trophic levels. The decline in a number of invertebrate taxa likely was caused by earthworm-mediated habitat changes (Maraun et al. 2003b), which suggests that indirect effects, such as habitat modification and other non-trophic interactions, need closer consideration in soil food web analyses.

The dampening of bottom-up effects is probably related to the peculiarity of the soil system (Dyer and Letourneau 2003). Intraguild predation, cannibalism, trophic-level-omnivory, strong connectivity and the heterogeneity of the soil matrix probably weaken bottom-up effects (Snyder and Wise 2001, Hart 2002, Rosenheim and Corbett 2003). Additionally, trophic levels in soil invertebrate communities are much less distinct than above the ground or in aquatic systems. Furthermore, natural variations in stable isotope ratios suggest that soil animal taxa do not form distinct trophic levels but a gradient from saprophagous to predatory species (Scheu and Falca 2000, Schneider et al. 2004). Even individual species feed on a wide range of food materials despite having preferences for specific food components when given the choice (Maraun et al. 2003a). The heterogeneity of the soil matrix and the limited possibility to move in the soil contributes to the dominance of generalist feeders in soil animal communities (Scheu 2002, Maraun et al. 2003a). As a consequence, the soil system is strongly buffered against perturbations in resource supply (Joergensen and Scheu 1999, Wardle 2002).

To conclude, we found that neither the amount nor the quality of resources strongly influence the soil food web structure. Bottom-up effects are therefore of very limited importance for most soil animals. The reason for that may be the importance of indirect

effects such as the burrowing activity of large decomposers that override bottom-up effects. These indirect effects probably contribute to the generally strong buffering capacity of the soil system against a number of external factors like resource addition, acidification, flooding and mechanical disturbances (Maraun et al. 2003b).

Appendix

List of oribatid mite species, families and groups analysed in this study. Oribatid mite species were ascribed to higher taxonomic levels (Enarthronota, Desmonomata, Mixonomata, *Tectocepheus*, Oppiidae, Suctobelbidae, Poronota, others).

Oribatid mites: Enarthronota: Brachychthoniidae (several species), *Eniochthonius minutissimus* (Berlese), *Hypochthonius rufulus* C.L. Koch; Desmonomata: *Nanhermannia coronata* Berlese, *Nothrus silvestris* Nicolet, *Platynothrus peltifer* (C.L. Koch); Mixonomata: Ptyctima (several species); *Tectocepheus*: *Tectocepheus minor* Berlese, *T. sarekensis* Trägardh, *T. velatus* (Michael); Oppiidae: *Berniniella bicarinata* (Paoli), *Dissorhina ornata* (Oudemans), *Medioppia subpectinata* (Oudemans), *Oppia sigma* Strenzke, *Oppiella nova* (Oudemans); Suctobelbidae (several species); Poronota: *Chamobates voigtsi* (Oudemans), *Hemileius initialis* (Berlese); Others: *Adoristes poppei* (Oudemans), *Carabodes* spp., *Cepheus dentatus* (Michael), *Dameobelba minutissima* (Sellnick)

CHAPTER 3 GENERAL DISCUSSION

Mites are the most diverse and abundant group of arachnids; until today about 100,000 arachnid species have been described from which ~50,000 species belong to the Acari (Cracraft and Donoghue 2004). Two-thirds of the mite species live in the soil system (Brussaard et al. 1997). Oribatid mites are one of these soil living mite taxa. Their species number is high (10,000 described species) and their abundance in most forest ecosystems is also high (up to 400,000 ind/m² in acidic forests) which makes them an important component of the edaphic fauna (Lebrun 1977).

Bernini (1986) proposed that the great diversification in Acari is based on their adaptive capacity. Lindquist (1975) stated that the Acari are rivalling the insects in evolutionary success due to their variety and quantity of ecological niches exploited in their history. Both assume that the high diversity of mites, especially that of oribatid mites, is a result of adaptive radiation. Adaptive radiations is defined as the outcome of divergent natural selection due to environmental factors, resources and resource competition (Schluter 2000). This ecological specialization results in species occupying different niches (Gittenberger 1991), and therefore co-occuring (sympatric diversity, Solem 1984). The most common examples for adaptive radiation are Darwin's finches, the African rift-lake chichlids, the Hawaiian silverwords and the Lake Baikal gammarids (Schluter 2000). Simpson (1953) even claimed that "adaptive radiation might explain all of life's diversity".

Another explanation for high species numbers, which is currently being hotly debated, is non-adaptive radiation. Non-adaptive radiation as an evolutionary diversification is not necessarily accompanied by niche differentiation, but caused by geographic barriers and/or restricted dispersal in sedentary organisms accomplished by genetic drift (allopatric diversity, Solem 1984; Diamond et al. 1976, Givnish et al. 1995). Gittenberger (1991)

argued that the species of the taxon *Albinari*a, a land snail of Greece, diversified via non-adaptive radiation. Adaptive radiation cannot be assumed a priori, rather, non-adaptive radiation is the logical null hypothesis (Schluter 2000, Hubbell 2005). Demonstrating niche diversifications on one of the n-axes of the n-dimensional Hutchinsonian niche space (Hutchinson 1957) can falsify this hypothesis (Schön and Martens 2004). The aim of this study was to investigate if the null hypothesis of oribatid mite diversity, i.e. non-adaptive radiation, can be rejected by testing for niche differentiation in these mites.

I focussed on trophic niche differentiation among oribatid mite species to investigate the extent to what trophic relationships may contribute to solving the enigma of the high number of oribatid mite species which coexist without obvious niche differentiation. In addition, other mechanisms which may influence the diversity of oribatid mites, such as disturbance or the quantity and quality of resources, were investigated.

3.1. Trophic niche differentiation in oribatid mites

Niche differentiation concerning food resources is one potential mechanism which may lead to reduced competition between species and therefore allow the coexistence of oribatid mite species in a homogeneous habitat, such as the soil. In this study trophic niche differentiation of oribatid mites was investigated in two laboratory food choice experiments and under 'natural' conditions analysing variations in stable isotope ratios ($^{15}N/^{14}N$) in oribatid mites extracted from four different forests.

Previous studies demonstrated that oribatid mites preferentially feed on fungi with dark melanised hyphae and/or spores ('Dematiacea') such as *Cladosporium*, *Alternaria* and *Ulocladium* (Luxton 1966, Mitchell and Parkinson 1976, Hedlund et al. 1991, Klironomos and Kendrick 1996, Maraun et al. 1998a, b, 2003a). In the first food choice experiment of my study oribatid mite species fed on different saprophytic fungal species ('Dematiacea'). However, most species preferentially fed on *Alternaria alternata* and *Ulocladium* sp.

indicating that niche differentiation concerning different 'Dematiacea' are of limited value for the understanding and explanation of high species numbers of oribatid mites. (CHAPTER 2.1.).

Mycorrhizal fungi in soil mainly belong to the arbuscular mycorrhizal fungi (AMF) or to ectomycorrhizal fungi. Feeding preferences of collembolans and oribatid mites on AMF are well studied (Klironomos and Kendrick 1996, Klironomos et al. 1999) but the findings of those studies are controversial (Gange 2000). In contrast, feeding of oribatid mites on ectomycorrhizal fungi has never been investigated. Here I present for the first time a feeding choice experiment using oribatid mites and ectomycorrhizal fungi (CHAPTER 2.2.). I could show that oribatid mites generally feed on ectomycorrhizal fungi. However, the results in part are contradictory; on one hand feeding preferences of oribatid mites significantly differed between species, but on the other hand most species preferentially grazed on two species, *Hymenoscyphus ericae* and *Boletus badius*. These results indicate that trophic niche differentiation contribute little to the high number of oribatid mites in soil.

Analysis of the natural variation in stable isotope ratios in animal tissue has shown to be a powerful tool in evaluating the trophic structure of animal communities (Minagawa and Wada 1984, Post 2002, McCutchan et al. 2003, Vanderklift and Ponsard 2003). Scheu and Falca (2000) and Ponsard and Arditi (2000) were the first who analysed soil animal communities using the nitrogen stable isotope ^{15}N. My study was the first detailed analyses of a large number of oribatid mite species (36 species/taxa) using ^{15}N for the analysis of trophic niche differentiation of oribatid mites and for the estimation of the number of trophic levels in oribatid mites (CHAPTER 2.3.). Signatures of $\delta^{15}N$ formed a gradient spanning over 12 delta units suggesting that different species occupy very different trophic niches. Additionally, the data suggest that oribatid mites form at least four feeding guilds: (1) phycophages/fungivores, (2) primary decomposer, (3) secondary decomposer and (4)

carnivores/scavengers/omnivores. Furthermore, the results documented that the trophic niches of oribatid mites are independent of the habitat the animals live in. Obviously, trophic niche differentiation in oribatid mites strongly contributes to the high diversity of this animal group.

The results of the laboratory feeding choice experiments indicate a lack of specialisation in oribatid mite feeding. This may be a consequence of the patchy and temporally limited occurrence of fungi in the field. Strong specialisation of the oribatid mite species on specific food resources may have been a dead end in evolution. The limited food specialization indicated by laboratory studies is in contrast to the results of the stable isotope analysis which indicate that oribatid mites occupy distinct and clearly separated trophic niches on the forest floor. Trophic niche differentiation of oribatid mite species may be due to (1) differential selection of fungal species in the field, (2) differential digestion of food resources and or (3) specialization on fungal species, which are difficult to cultivate in the laboratory. In this study, only a small amount of fungi, which occur in the field, were tested as food for oribatid mites. Furthermore, differences in stable isotope signatures in oribatid mite species may be due to feeding on different mixtures of fungal species, detritus and animal prey. Overall, the term ‘choosy generalists’ well characterises the trophic strategy of oribatid mite species.

The investigations on the feeding biology and trophic niche differentiation of oribatid mites support the hypotheses that oribatid mites underwent an adaptive radiation. However, the co-evolutionary patterns between oribatid mites and food resources are weaker than those between e.g. plants and herbivores or pollinating insects.

3.2. The effect of disturbance and resource addition on oribatid mite diversity

Disturbances of intermediate levels may prevent competition between species and therefore promote species diversity (intermediate disturbance hypothesis; Connell 1978). Results of studies which investigated the effect of disturbances in aquatic systems supported this hypothesis (Sousa 1979, Townsend et al. 1997). In soils, earthworms act as ecosystem engineers (Lawton 1994) and may disturb the microarthropod community (Scheu and Schulz 1996, Maraun et al. 1999). Therefore, I studied the influence of earthworm activity on the diversity of oribatid mites in a field experiment (CHAPTER 2.4.). Results of this study did not support the intermediate disturbance hypothesis. Oribatid mite diversity uniformly declined with increasing disturbance. Oribatid mites are sensitive to disturbance due to their life history; they reproduce very slowly and their dispersal ability is low. Therefore, it is plausible that oribatid mite diversity did not profit from intermediate disturbances.

It is hypothesised that the addition of resources results in higher diversity in bottom-up controlled communities, due to reduced resource competition. Detritus-based food chains are often considered as typical examples for bottom-up controlled systems (Pimm 1982). Since most oribatid mite species are detritivores, I investigated the influence of resource addition on oribatid mite diversity and density in a field experiment (CHAPTER 2.5.). Results of this experiment indicated that the addition of different types of resources did not affect oribatid mite diversity or density, with the exception of the CNP treatment, where the density of oribatid mites increased. The slightly higher abundance of oribatid mites in the CNP treatment could be explained by the decrease in earthworm density in this treatment. However, the diversity of oribatid mites did not change in the CNP treatment, which indicates that resource addition did not alter species richness of oribatid mites.

Results of the two latter experiments indicate that intermediate levels of disturbance and resource addition do not contribute to the high diversity of oribatid mites in forest ecosystems. However, both experiments documented that earthworm activity has a strong negative effect on oribatid mite diversity and density. Disturbances by earthworms presumably are more important factors affecting oribatid mite community structure than other biotic or abiotic factors. This suggestion is supported by the results of other studies, which also documented the detrimental effect of earthworms on soil microarthropod communities (Maraun et al. 1999, McLean and Parkinson 1998, 2000, Maraun and Scheu 2000). However, further resource addition studies, e.g. microcosm experiments where earthworms are excluded, have to be performed to answer the question to what extent oribatid mites are bottom-up controlled.

3.3. Prospects

There is considerable progress in understanding the feeding biology and trophic niche differentiation in oribatid mites. Oribatid mites feed on a wide variety of resources, including algae, lichens, litter, fungi and other (dead or living) soil animals, and they selectively feed on saprophytic and mycorrhizal fungi offered in laboratory food choice experiments. Additionally, results of stable isotope analysis strongly indicate trophic niche differentiation in oribatid mites. To understand the factors that form these niches, further studies should investigate the feeding habits of this soil animal group using more sophisticated techniques, such as fatty acid analysis of the animal tissue or molecular analysis of gut contents.

Fatty acid patterns (PLFA and NLFA) have been used to classify microorganisms in soil (Tunlid and White 1992, Zelles 1999) and to estimate fungal biomass (Frostegård and Bååth 1996, Mikola and Setälä 1998). Recently, fatty acids were suggested as a tool to investigate food relationships in soil food webs. Ruess et al. (2002) reported for nematods

that the lipid composition is controlled by both the nematode species and its diet. Studies on the fatty acid pattern of collembolans and their diet indicated that neutral lipids (NLFA) are promising biomarkers for trophic niches (Haubert 2004). Therefore, the analysis of fatty acid patterns of oribatid mite species may help to clarify their niche differentiation and may therefore contribute to the understanding of the high diversity of oribatid mites.

The analysis of the gut content using molecular markers is one of the most sophisticated methods available for studing the feeding biology of animals. Agusti et al. (2003) showed that collembolans can be detected in the gut of their predators (spiders) using molecular markers (COI). Surprisingly, this method has not been used to investigate the food of oribatid mites and other soil decomposer animals. The advantages of this method compared with other methods, especially for soil animals such as oribatid mites, are that (1) fungi can be detected on species level, (2) organisms remain of putative oribatid mite prey, such as nematodes and bacteria, can be detected and (3) even small amounts of prey (e.g. fungi, lichens or animal remains) can be detected.

Other mechanisms than trophic niche differentiation, resource addition or disturbance may also be responsible for the high diversity of oribatid mites, e.g. habitat heterogeneity and top-down control. The spatial or habitat heterogeneity hypothesis predicts that the more heterogeneous and complex the physical environment, the more complex and the higher the diversity of species (Brown 1998). However, this assumption does not necessarily apply to all animal groups. Giller (1996) emphasized that spatial heterogeneity is a driving factor for the diversity of soil animal communities. Anderson (1978) investigated the relationship between oribatid mites and the diversity of soil and litter microhabitats. He pointed to a significant correlation between oribatid mite diversity and microhabitat diversity. Other studies on the effect of habitat heterogeneity on oribatid mite diversity support these results (André 1985, Behan-Pelletier and Walter 2000, Hansen

2000, Karasawa and Hijii 2004). In contrast, Migge et al. (1998) did not find differences in the diversity and density of oribatid mites between beech, spruce and mixed forest stands suggesting that different litter materials and the associated differential structure of the soil habitat is of little importance for oribatid mite community structure. Additionally, the results of the study of Maraun et al. (1999) did not support the hypotheses that earthworm middens as microhabitats contribute to the high diversity of oribatid mites. Future experiments on other microhabitats of oribatid mites, such as the bark of trees and soil pores of different size, may clarify the importance of microhabitat heterogeneity for oribatid mite diversity.

The top-down model of population regulation postulates that predation controls the community structure of the prey via trophic cascades. Hairston et al. (1960) stated that 'the world is green' because predators regulate herbivores which leads to reduced herbivory and results in plants attaining densities at which they become resource limited. Detritus based food chains are often considered as typical examples of bottom-up controlled systems, because the detritivores do not affect the renewal rate of their food (Pimm 1982, Begon et al. 1995). Ponsard et al. (2000) argued that bottom-up control in the detritus-detritivore interaction does not preclude the possibility of top-down effects at higher trophic levels. Some studies investigated whether soil systems are predominately top-down or bottom-up controlled (e.g. Mikola and Setälä 1997, 1998, Scheu and Schaefer 1998, Ponsard et al. 2000), but only few studies focussed on the effect of both factors on diversity patterns (Salamon et al. 2005). In this study (CHAPTER 2.5.) resource addition did not affect species richness of oribatid mites, which implies that oribatid mites may be regulated by predators, such as gamasid mites, carabid and staphylinid beetles or other macroarthropods. In the future, experimental studies are needed which investigate the regulatory effect of predators on oribatid mite diversity.

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LEBENSLAUF

Persönliche Daten

Name:	Katja Schneider
Geburtstag:	12.09.1974
Geburtsort:	Darmstadt, Deutschland

wissenschaftlicher Werdegang

1981 - 1987	Grundschule in Darmstadt (Elly-Heuss-Knapp-Schule)
1987 - 1991	Realschule in Darmstadt (Mornewegschule)
1991 - 1994	Gymnasiale Oberstufenschule in Darmstadt (Bertholt-Brecht-Schule)
15.06.1994	Abitur
1994 - 1998	Grundstudium Biologie an der Technischen Universität Darmstadt
1998 - 2001	Hauptstudium Biologie an der Technischen Universität Darmstadt Schwerpunkte Ökologie, Zoologie und Tierphysiologie
10.12.2001	Diplom in Biologie Thema der Diplomarbeit: „Der Einfluss von Habitatfragmentierung, Sonneneinstrahlungsintensität und winterliche Staunässe auf die Mikroarthropoden-Gemeinschaft eines Stieleichen-Hainbuchenwaldes.“
seit 04.2002	Promotionsstudium im Fachbereich Biologie an der Technischen Universität Darmstadt gefördert durch die Deutsche Forschungsgemeinschaft im Rahmen des Schwerpunktprogramms “Radiationen-Genese biologischer Diversität” (SPP 1127) mit dem Thema “Radiation in sexual and parthenogenetic oribatid mites”

Fortbildungen und Fachtagungen

27. - 28.01.2003	Invitation to the 2nd Priority Programme Colloquium of the DFG (SPP 1127) in Bad Honnef; Vortrag
09. - 13.06.2003	96. Jahresversammlung der Deutschen Zoologischen Gesellschaft in Berlin; Vortrag
13. - 15.06.2003	5. GEO-Tag der Artenvielfalt im Nationalpark Harz/Hochharz; Erfassung der Milbendiversität
26. - 28.09.2003	4. Milbenkundliches Kolloquium in Greifswald; Poster

20. - 21.10.2003	2nd Call for the Proposals for the DFG Priority Programme 1127 in Wernigerode; Vortrag
22.03. - 02.04.2004	DNA-Taxonomie-Workshop in Köln
17. - 20.04.2004	CONSIDER workshop and PhD Course 'Fragmented habitats and temporal and spatial dynamics of organisms on micro- to landscape scale'; Vortrag
13. - 14.05.2004	Annual Colloquium of the SPP 1127 (DFG) in Bad Honnef; Vortrag
21.06. - 03.07.2004	54th Annual Acarology Summer Program, Soil Acarology (Mesostigmata & Oribatida) in Columbus (Ohio, USA)
26. - 30.07.2004	5th Symposium of the European Association of Acarologists (EURAAC) in Berlin; Vortrag
30.08. - 03.09.2004	XIVth International Colloquium on Soil Zoology and Ecology, Rouen (Frankreich); Vortrag

Mitglied der AG Bodenmesofauna

14. - 16.03.2001	17. Jahrestreffen in Gießen; Vortrag
13. - 15.03.2002	18. Jahrestreffen in Darmstadt; Organisation des Treffens & Vortrag
23. - 25.04.2003	19. Jahrestreffen in Wien (Österreich); Vortrag
06. - 09.04.2005	21. Jahrestreffen in Göttingen; Vortrag

berufliche Tätigkeiten

1997 - 1998	studentische Hilfskraft an der Technischen Universität Darmstadt, Fachbereich Biologie: Praktika-Betreuung am Institut für Zoologie
2001, 2004 - 2005	freie Mitarbeiterin bei der Firma Bio-Test Labor Sagerheide; Acarologin
01. - 03.2002	wissenschaftliche Hilfskraft an der Technischen Universität Darmstadt, Fachbereich Biologie: Milbenbestimmung und Datenanalyse am Institut für Zoologie, AG Scheu

Darmstadt, den 13. Mai 2005

EIDESSTATTLICHE ERKLÄRUNG

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Dissertation selbstständig und nur mit den angegebenen Hilfsmitteln angefertigt habe. Die Daten zu anderen Tiergruppen als Oribatida, Prostigmata und Uropodina in Kapitel 2.4. und 2.5., wurden nicht von mir erhoben, sondern stammen von meinen Koautoren J.-A. Salamon und M. Maraun (Salamon et al. 2005 und Maraun et al. 2003).

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Katja Schneider